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NATURAL HISTO

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P. J. K. BURTON

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 27 No. 1
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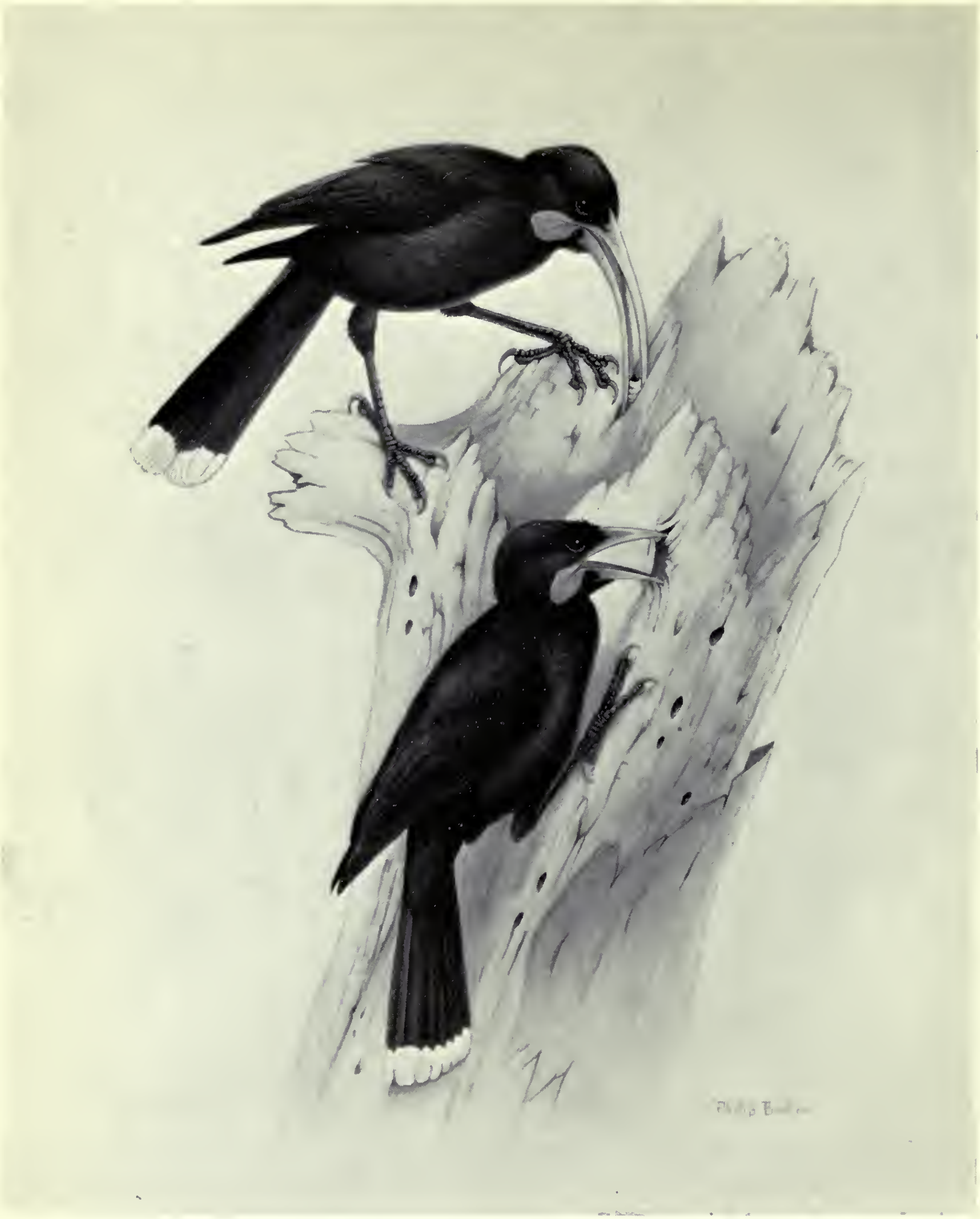

Frontispiece. Male and female Huias (*Heteralocha acutirostris*) showing probable feeding methods. The male is depicted excavating decayed wood by the 'gaping' technique described in the text.

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BY

PHILIP JOHN KENNEDY BURTON

Pp 1–48 ; 1 *Plate*, 26 *Text-figures*

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ANATOMY OF HEAD AND NECK IN THE HUIA *(HETERALOCHA ACUTIROSTRIS)* WITH COMPARATIVE NOTES ON OTHER CALLAEIDAE

By PHILIP J. K. BURTON

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SYNOPSIS

Spirit specimens and skeletons of the Huia (*Heteralocha acutirostris*) have been used in a detailed study of feeding adaptations in this extinct species. The Huia showed remarkable sexual dimorphism in bill form, and particular attention is paid throughout to differences between male and female. Comparison is made with the other members of the Callaeidae – *Creadion carunculatus* and *Callaeas cinerea*. The features studied indicate that the Huia was highly specialized for feeding by 'gaping' in decayed timber, in order to gain access to beetle grubs. The full extent of sexual dimorphism revealed by this study is reviewed, and its significance is discussed.

I. INTRODUCTION

The extinct Huia (*Heteralocha acutirostris*) of New Zealand is frequently quoted as an example of extreme sexual dimorphism among birds. This dimorphism is shown most conspicuously by the bill, which in the male was typically fairly straight, moderately long, and tapered evenly to a point ; while in the female it was much longer, more slender, and strongly downcurved. There is little information on the extent of dimorphism beyond this. Phillipps (1963) mentions plumage differences and a tendency towards stronger claws in older males, and Selander (1966) gives bill, wing and tarsus measurements for a small sample of each sex. The anatomical study of the Huia by Garrod (1872) concentrated principally on establishing the affinities of the species, and did not inquire closely into its sexual dimorphism. The problem of its relationships is still not fully resolved beyond the fact that the Huia is closely related to two other New Zealand species – the Saddleback (*Creadion* *carunculatus*) and the Kokako (*Callaeas cinerea*) (Stonor, 1942). The three together form the family *Callaeidae*, placed between the Dicruridae and Grallinidae by Mayr and Greenway (1956) ; close affinity with the Sturnidae has been suggested in the past (Garrod, 1872 ; Gray, 1870).

The present investigation has been concerned with the anatomical basis of the Huia's feeding specializations. In particular, I have attempted to discover the full extent of sexual dimorphism in feeding structures, and to correlate this where possible with bill form and feeding methods. It is thus a study of adaptation, unusual in that the principal forms to be compared are the two sexes of a single species. The material on which the investigation is based is contained in the avian anatomical collections of the British Museum (Natural History). These consist of six spirit and one osteological specimens of the Huia, one spirit specimen of the Saddleback and four spirit specimens of the Kokako. It is thought that the Huia spirit specimens may be the only fluid-preserved examples of this species in existence, although there is at least one skeleton in New Zealand (Phillipps, 1963) and another in the U.S.A. (Bock, 1960a).

The history of the Huia's disappearance, and many aspects of its life and habits, are summarized by Phillipps. Last reported alive in 1907, it is probable that some survived after this date, and Phillipps entertains the possibility that a few may still exist. Its range was restricted to the mountainous Wellington Province of North Island, New Zealand. Here, the combination of a mild climate and heavy rainfall has produced densely forested country with a high incidence of timber decay and epiphytic growth. The Huia fed principally on insects, varied with some vegetable matter, but by far the most important prey appears to have been the larvae of the Huhu beetle, *Prionoplus reticularis* (Cerambycidae). This large beetle is common in many parts of New Zealand, and its larvae, found in decaying timber, may reach a length of 70 mm and a width of 20 mm. The most detailed account of the Huia's manner of extracting these is provided by Buller (1888). This account has been often quoted, but because of its relevance to the present study, it seems essential to do so again. Buller's description refers to a pair of captive Huias which at first he fed on individual huhu grubs :

> 'On offering one of these to the Huia he would seize it in the middle, and, at once transferring it to his perch and placing one foot firmly upon it, he would tear off the hard parts, and then throwing the grub upwards to secure it lengthwise in his bill, would swallow it whole . . . They seemed never to tire of probing and chiselling with their beaks. Having discovered that the canvas lining of the room was pervious, they were incessantly piercing it, and tearing off large strips of paper, till, in the course of a few days, the walls were completely defaced.
>
> But what interested me most of all was the manner in which the birds assisted each other in their search for food, because it appeared to explain the use, in the economy of nature, of the differently formed bills in the two sexes. To divert the birds, I introduced a log of decayed wood infested with the huhu grub. They at once attacked it, carefully probing the softer parts with their bills, and then vigorously assailing them, scooping out the decayed wood till the larva or pupa was visible, when it was carefully drawn from its cell, treated in the way described above, and then swallowed. The very different development of the mandibles in the two sexes enabled them to perform separate offices. The male always attacked the more decayed portions of the wood, chiselling out his prey after the manner of some Woodpeckers, while the female probed with her long pliant bill the other cells, where hardness of the surrounding parts resisted the

chisel of her mate. Sometimes I observed the male remove the decayed portion without being able to reach the grub, when the female would at once come to his aid, and accomplish with her long slender bill what he had failed to do. I noticed, however, that the female always appropriated to her own use the morsels thus obtained.'

An additional reference to the different feeding techniques of male and female is the note by J. M. Wright quoted by Oliver (1955):

> 'I have watched them in pairs hunting for wetas.* The male would tear away at the outer part of a green sapling. The female then tried to retrieve the weta with her long slender bill. If not successful she would stand back while the male tried to enlarge the hole. Unless the tree was a maire the birds would generally succeed and would then fly away with the weta.'

Phillipps (1963) also provides the most detailed information available on the extent of dimorphism ascertainable from skins, and on the range of variation in the two sexes, based on 119 specimens in New Zealand museums. Young birds show little difference in size and shape of the bill. Some male bills were more curved than usual, but were normally deeper than those of females. The male bills reached an extreme length of 59–60 mm (from feathers), and females up to 104 mm. Phillipps mentions two doubtful cases of birds with bills 63 mm long which he has treated as males, though they may be females. The skin collection of the British Museum (Natural History) includes two doubtful individuals ; one, with a bill length of 76·4 mm is labelled as a male ; the other, labelled as a female, has a bill of 71·8 mm. Excluding these, bill length data for other specimens in the collection may be summarized as follows :

Males :	Mean 59·7 ;	Min. 54·7 ;	Max. 65·0	(16 specimens).
Females :	Mean 96·3 ;	Min. 87·1 ;	Max. 108·0	(7 specimens).

Buller (1878) also gives details on the range of bill form in the Huia and figures several specimens, including a female with the upper jaw much longer than the lower, recalling some species of *Hemignathus* (Drepanididae).

II. METHODS AND MATERIAL

Most of the observations reported here were obtained simply by dissection using a stereomicroscope at powers mainly in the range ×2½ to ×20. The main complicating factor was the irreplaceable nature of the Huia specimens, and because of this, it was thought prudent to keep dissections of this species to a minimum. In general, dissections have been limited to the left side, and as little structure as possible has been removed. Because of its history, the single specimen of *Creadion carunculatus* was regarded as of similar value, and no dissections were attempted which would have required removing or severing structures.

For convenient reference, the Huia specimens were given a simple individual coding in addition to their British Museum (Natural History) Registration numbers.

---

* Orthoptera, Gryllacridoidea.

Details of the specimens of Callaeidae used, with their conditions at commencement of the study, are as follows :

Heteralocha acutirostris

♂ 1. Reg. No. A 1973.1.3. Intact spirit specimen.
♂ 2. Reg. No. A 1973.1.2. Intact spirit specimen.
♂ 3. Reg. No. 1940.12.8.107. Intact spirit specimen.
♂ 4. Reg. No. 81.1.17.91. Complete skeleton specimen.
♀ A. Reg. No. A 1973.1.4. Spirit specimen with skull almost completely skeletonized. Rhamphotheca of upper jaw retained (but detached), tongue, hyoid muscles, M. depressor mandibulae and all neck muscles intact.
♀ B. Reg. No. A 1973.1.1. Spirit specimen with cranium and upper jaw completely skeletonized, removed and maintained as dried specimen. Upper jaw broken and rhamphotheca missing. Lower jaw with rhamphotheca intact, detached, but retained in spirit. Tongue, hyoid muscles and all neck muscles intact.
♀ C. Reg. No. 1940.12.8.108. Intact spirit specimen.

Creadion carunculatus

Reg. No. 1845.2.21.392. Spirit specimen with skull detached and skeletonized except for M. depressor mandibulae which is intact. Rhamphotheca of both jaws missing. Tongue, hyoid muscles and all neck muscles intact. This specimen is believed to have been collected on Captain Cook's third voyage (Burton, 1969). It is probably the oldest surviving spirit specimen of any bird, but is in good condition.

Callaeas cinerea

Reg. Nos. A 1973.1.5 and A 1973.1.6. 2 intact spirit specimens.

Various spirit, skeleton or skin specimens of birds in other families were also examined for comparative purposes. The species involved are mentioned in the text or in the tables.

III. SKULL AND LIGAMENTS

The skull of a male Huia was described and figured by Garrod (1872), who called attention to some of its conspicuous features. A short description of the skull is also given by Oliver as an appendix to the book by Phillipps (1963). The skulls of male and female specimens are depicted in Figs. 1–3. It will be noted that with the rhamphotheca removed, the disparity between the sexes in jaw form appears much less than in skin specimens ; this is due to the much greater development of the rhamphotheca in the female. Striking features of the skull in both sexes (though more marked in the male) are the prominent occipital crest, well-developed exoccipital process and very long retroarticular process. Less obvious, but equally

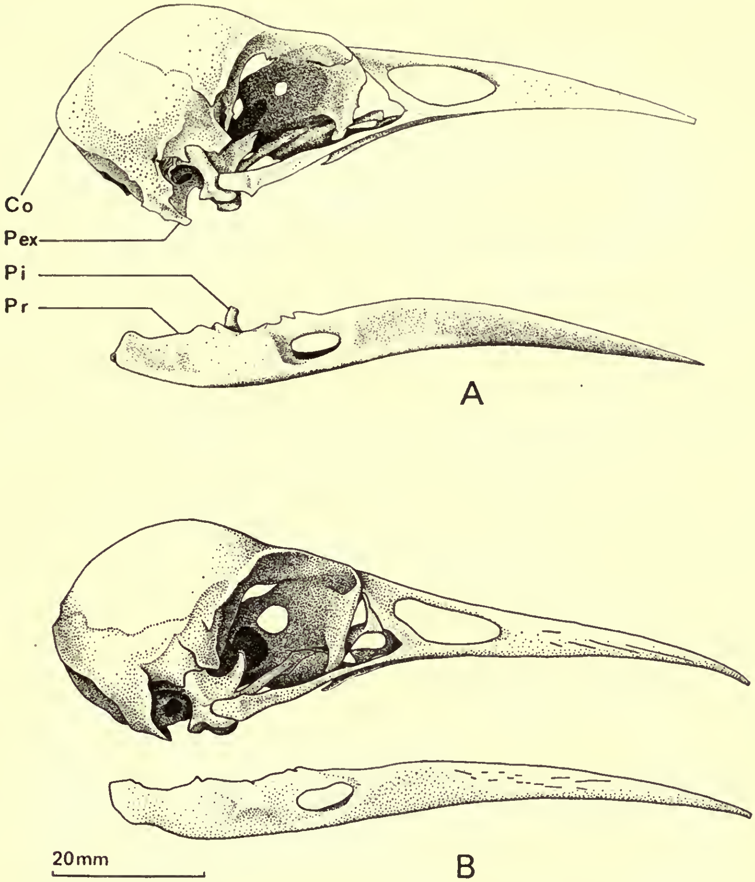

Fig. 1. *Heteralocha acutirostris*, skull in lateral view. A. Male (♂ 4). B. Female (♀ A). For abbreviations see p. 47.

unusual, is the position and form of the nasal-frontal hinge. The nasals extend backward in the form of a rounded spur, reaching a point roughly level with the middle of the orbits. The nasal-frontal hinge is consequently situated much further posteriorly than in typical passerines; the drawings of *Creadion* and *Callaeas* (Figs. 4–9) show the normal condition.

Quantitative data for the specimens studied are summarized in Table 1. Relative values for the various measurements taken have been assigned by giving for each its ratio to length of the jugal bar. Several other ratios are also included. In the absence of weight data, sternum length is used as a crude index of body size (Amadon, 1943; Zusi, 1962); measurements of wing, tail and tarsus are also given (*R* to *U*).

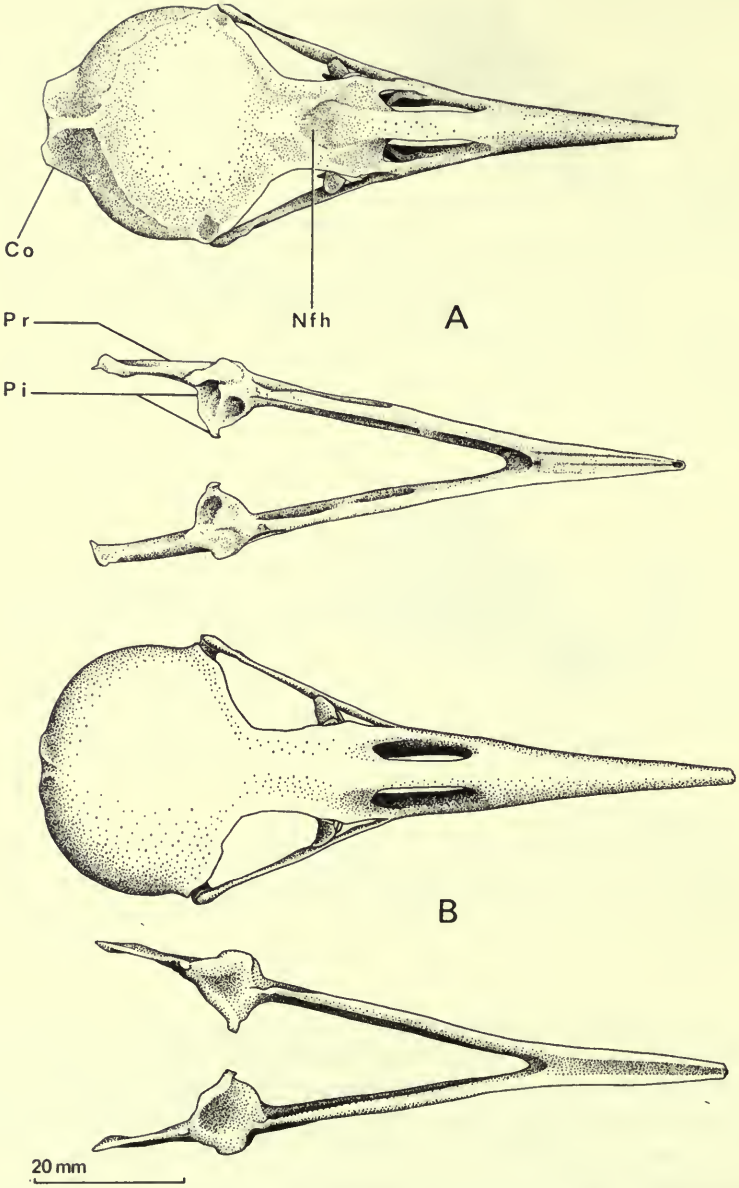
Co
Nfh
A
Pr
Pi
B
20 mm

Fig. 2. *Heteralocha acutirostris*, skull in dorsal view.
A. Male (♂ 4). B. Female (♀ A). For abbreviations see p. 47.

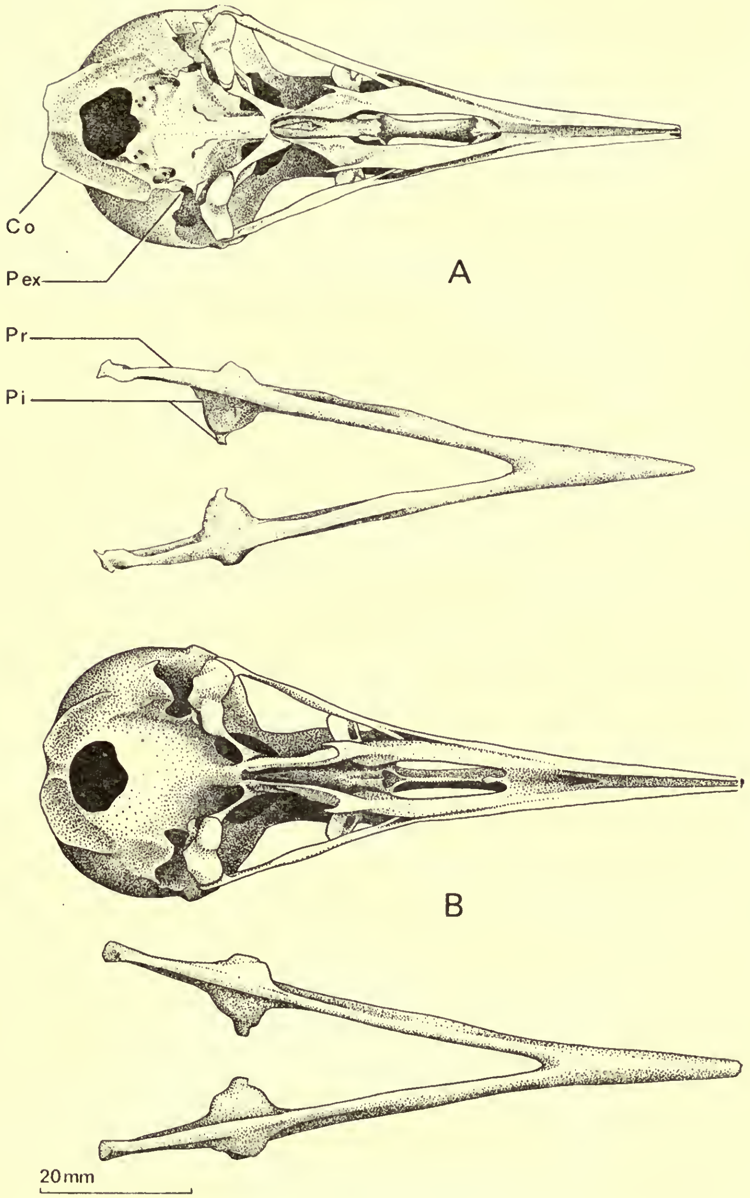
Co
Pex
A
Pr
Pi
B
20mm

Fig. 3. *Heteralocha acutirostris*, skull in ventral view.
A. Male (♂ 4). B. Female (♀ A). For abbreviations see p. 47.

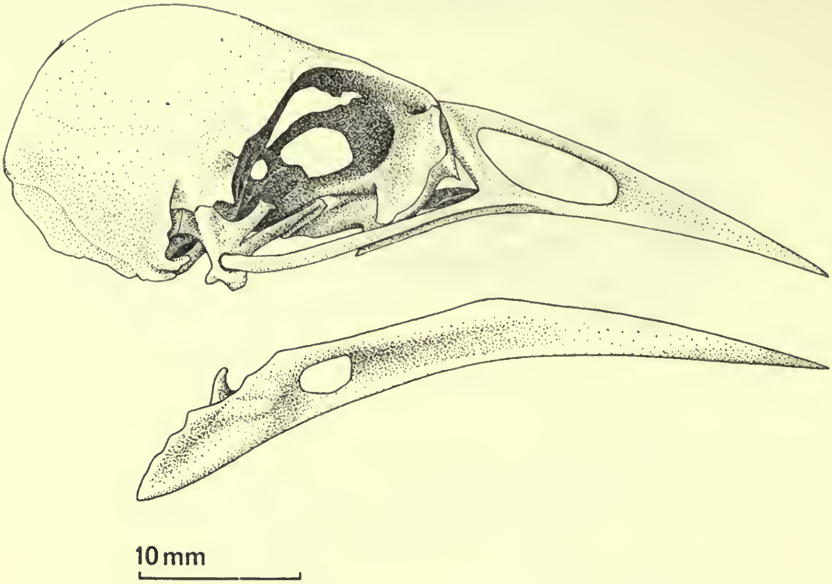

FIG. 4. *Creadion carunculatus*, skull in lateral view.

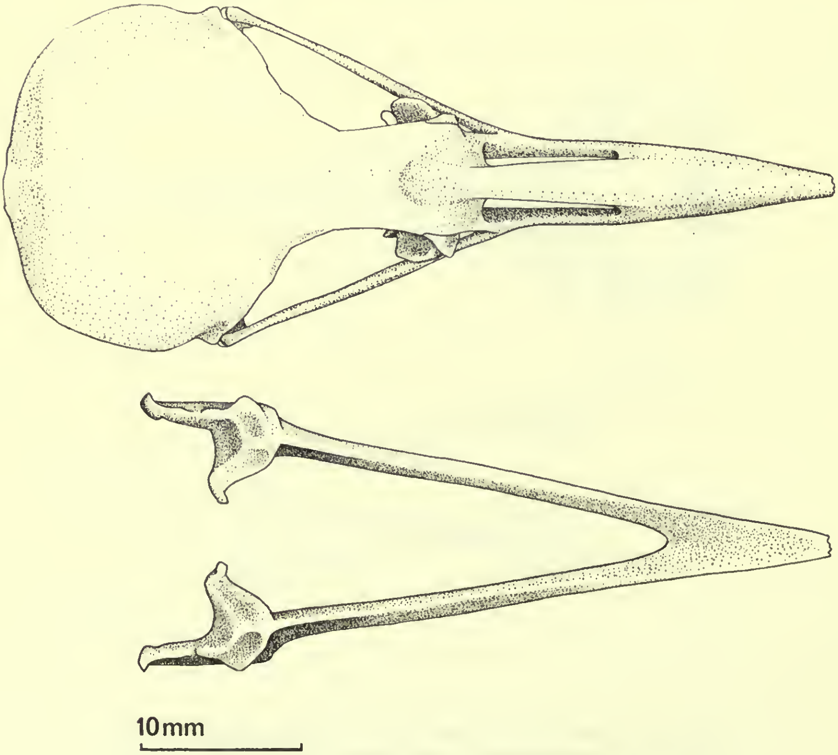

FIG. 5. *Creadion carunculatus*, skull in dorsal view.

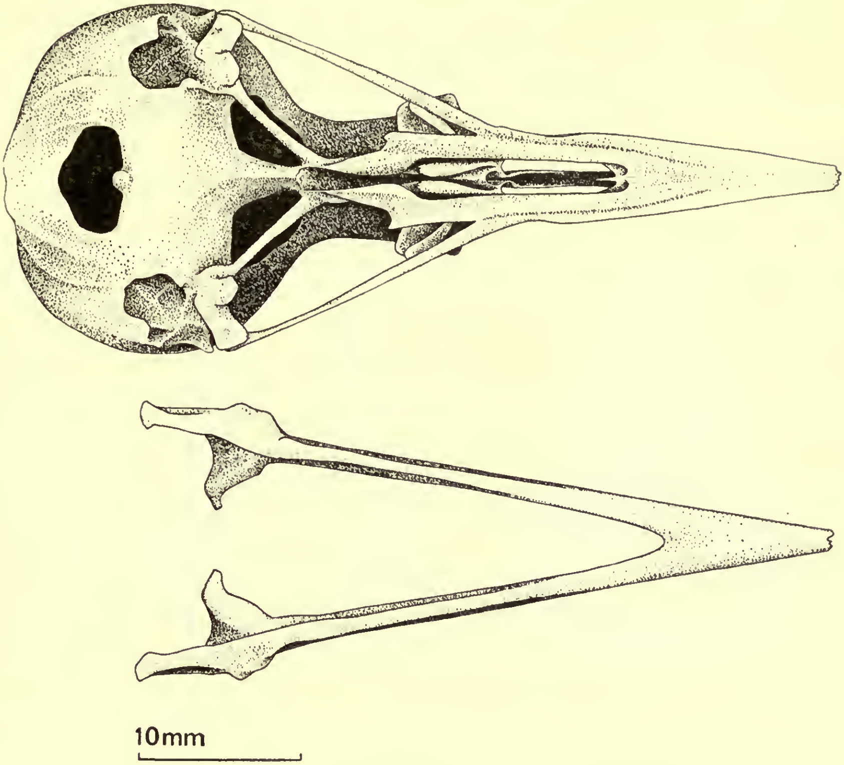

Fig. 6. *Creadion carunculatus*, skull in ventral view.

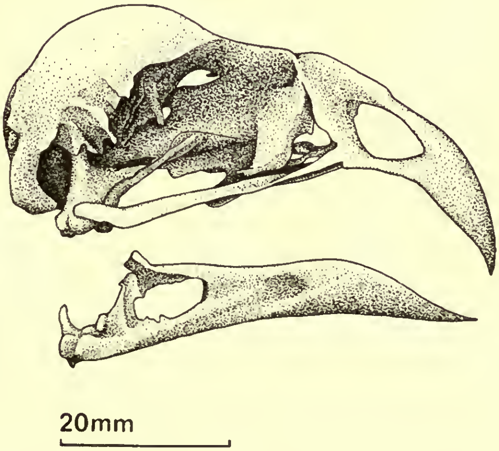

Fig. 7. *Callaeas cinerea*, skull in lateral view.

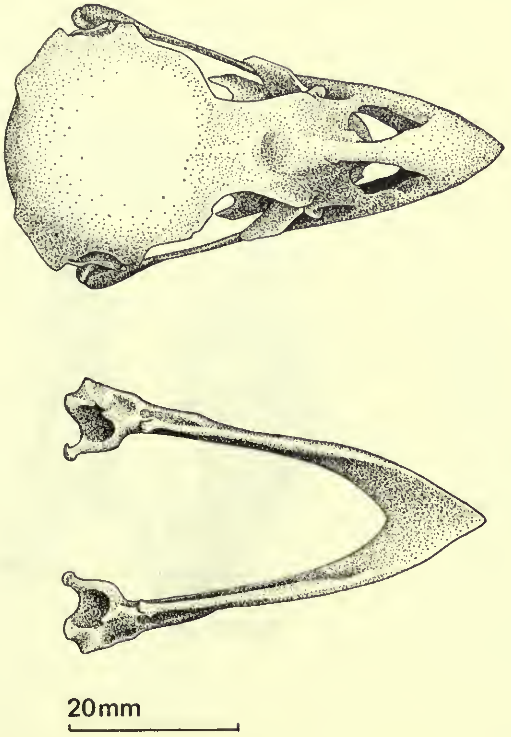

Fig. 8. *Callaeas cinerea*, skull in dorsal view.

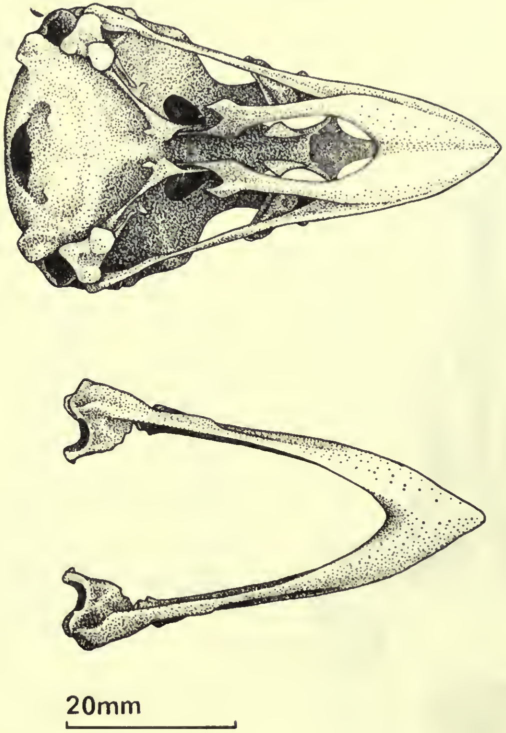

Fig. 9. *Callaeas cinerea*, skull in ventral view.

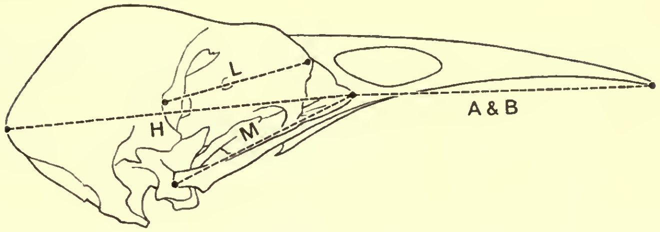

FIG. 10. Skull of *Heteralocha acutirostris* showing the method of taking various measurements given in Table 1. For key see below.

The methods by which skeleton measurements were taken are as follows:

A Upper jaw length: Fig. 10.
B Upper jaw with rhamphotheca removed: Fig. 10.
C, *D* Lower jaw: tip of mandible to posterior tip of retroarticular process, with and without rhamphotheca.
E Retroarticular process: measured from the posterior edge of the lateral condyle of the quadrate.
F Bill depth: measured at right angles to the tomia, level with the junction of nasal and jugal bars. Only given for specimens with rhamphotheca intact on both jaws.
G Bill width: measured at the same point as *F*, with or without rhamphotheca.
H Cranium length: Fig. 10.
J Cranium breadth: the greatest breadth of the cranium (just posterior to the orbits).
K Anterior cranium breadth: the maximum breadth of the cranium anterior to the orbits.
L Orbit length: Fig. 10.
M Jugal bar: Fig. 10.
N Quadrate: from the lateral extremity of the articulation with the jugal bar, to the medial tip of the orbital process.
O Pterygoid: from the anterior to the posterior extremities visible in anterolateral view.
P Tongue length: from the anterior tip to the tips of the postero-lateral papillae.
Q Sternum length: from the midpoint of the posterior margin to the anteroventral tip of the keel.

The postorbital, internal jugo-mandibular and occipito-mandibular ligaments are present. Strong connective tissue running from the postorbital process to the ectethmoid process across the ventral lateral side of the orbit amounts to an ill-defined suborbital ligament. There is no external jugo-mandibular ligament. The occipito-mandibular ligament is extremely stout, and much of its central region is ossified, more so in male specimens. The internal jugo-mandibular ligament contains two

TABLE 1

Quantitative data for the specimens of Callaeidae used in this study

		Heteralocha ♂ 1	*Heteralocha* ♂ 2	*Heteralocha* ♂ 3	*Heteralocha* ♂ 4	*Heteralocha* ♀ A	*Heteralocha* ♀ B	*Heteralocha* ♀ C	*Heteralocha* Mean of ♂ specimens	*Heteralocha* Mean of ♀ specimens	*Creadion* 1845.2.21.392	*Callaeas* 1940.12.8.109	*Callaeas* (Bennett Esq.)
A	Upper jaw length	50·4 (1·83)	50·0 (1·80)	50·3 (1·82)	–	98·9 (3·73)	–	82·1 (3·17)	50·2 (1·82)	90·0 (3·45)	–	25·1 (0·78)	–
B	Upper jaw, rhamphotheca removed	(44·8) (1·63)	44·7 (1·61)	46·0 (1·66)	(38·6) (1·42)	48·4 (1·82)	–	51·0 (1·97)	43·5 (1·58)	49·7 (1·89)	23·0 (1·33)	24·5 (0·76)	20·2 (0·66)
$\frac{A-B}{A}$	Index of relative rhamphotheca development	0·11	0·11	0·09	–	0·51	–	0·38	0·10	0·45	–	0·02	–
C	Lower jaw length	91·9 (3·34)	88·3 (3·18)	87·9 (3·17)	–	–	108·9 (4·24)	110·1 (4·25)	89·4 (3·23)	109·5 (4·25)	–	51·0 (1·59)	–
D	Lower jaw, rhamphotheca removed	86·8 (3·16)	84·1 (3·03)	85·3 (3·08)	78·3 (2·88)	80·1 (3·02)	84·8 (3·30)	87·7 (3·39)	83·6 (3·04)	84·2 (3·24)	44·1 (2·55)	50·3 (1·57)	45·9 (1·49)
E	Retroarticular process	15·1 (0·55)	16·5 (0·59)	17·6 (0·63)	15·2 (0·56)	14·0 (0·53)	13·5 (0·53)	13·5 (0·52)	16·1 (0·58)	13·7 (0·53)	8·0 (0·46)	nil	nil
E/C	Retroarticular process relative to total lower jaw	0·16	0·19	0·20	–	–	0·12	0·12	0·18	0·12	–	–	–

F	Bill depth	20·5 (0·75)	19·7 (0·71)	19·5 (0·70)	–	–	–	16·5 (0·64)	19·9 (0·72)	16·5 (0·64)	9·8 (0·57)	19·6 (0·61)	17·8
G	Bill width	12·0 (0·44)	12·5 (0·45)	11·9 (0·43)	12·2 (0·45)	10·0 (0·38)	10·2 (0·40)	10·7 (0·41)	12·1 (0·44)	10·3 (0·40)	5·9 (0·34)	15·3 (0·48)	13·8 (0·58)
H	Cranium length	45·6 (1·66)	47·4 (1·70)	47·4 (1·71)	45·1 (1·66)	42·8 (1·61)	42·8 (1·67)	43·2 (1·67)	46·4 (1·68)	42·9 (1·65)	29·4 (1·70)	39·4 (1·23)	39·2 1·27
J	Cranium breadth	30·0 (1·09)	32·8 (1·18)	31·8 (1·15)	29·9 (1·10)	28·2 (1·06)	28·0 (1·09)	28·8 (1·11)	31·1 (1·13)	28·3 (1·09)	20·5 (1·18)	28·7 (0·89)	29·3 (0·95)
K	Anterior cranium breadth	14·8 (0·54)	13·7 (0·49)	13·4 (0·48)	13·9 (0·51)	12·0 (0·45)	11·7 (0·44)	11·9 (0·46)	13·9 (0·50)	11·9 (0·45)	8·4 (0·49)	15·6 (0·49)	14·8 (0·48)
L	Orbit length	19·2 (0·70)	18·4 (0·66)	19·0 (0·69)	18·5 (0·68)	18·4 (0·69)	17·7 (0·69)	17·8 (0·69)	18·8 (0·68)	18·0 (0·69)	12·5 (0·72)	20·2 (0·63)	21·0 (0·68)
M	Jugal bar length	27·5 (1·00)	27·8 (1·00)	27·7 (1·00)	27·2 (1·00)	26·5 (1·00)	25·7 (1·00)	25·9 (1·00)	27·5 (1·00)	26·0 (1·00)	17·3 (1·00)	32·1 (1·00)	30·8 (1·00)
N	Quadrate	13·3 (0·48)	13·4 (0·48)	–	1·36 (0·50)	12·5 (0·47)	12·4 (0·48)	11·9 (0·46)	13·4 (0·49)	12·3 (0·47)	7·3 (0·42)	12·7 (0·40)	–
O	Pterygoid length	–	–	–	13·6 (0·50)	14·1 (0·53)	13·2 (0·51)	–	13·6 (0·50)	13·6 (0·52)	7·4 (0·43)	16·5 (0·51)	–
P	Tongue length	31·5 (1·15)	29·9 (1·08)	31·7 (1·14)	–	30·1 (1·14)	31·8 (1·24)	32·1 (1·24)	31·03 (1·12)	31·3 (1·21)	–	21·4 (0·67)	18·2 (0·59)
Q	Sternum length	40·5	40·4	38·9	37·3	37·0	36·0	35·8	39·3	36·3	18·3	35·2	–
M/Q	Skull to body index	0·68	0·69	0·71	0·73	0·72	0·71	0·72	0·70	0·72	0·95	0·91	–
R	Culmen from feathers	59·8	57·2	57·2	–	108·0	–	99·6	58·1	103·8	–	–	–
S	Wing (maximum chord)	202	195	197	–	192	197	200	198	196	92	157	147
T	Tail	200	182	–	–	192	193	204	91	196	76	154	–
U	Tarsus	86·3	83·1	80·5	82·4	76·5	78·8	75·8	83·1	77·0	37·0	68·7	67·6

Each head measurement is followed (in brackets) by its ratio to jugal length. Blank spaces indicate that measurements could not be made owing to missing structures or the presence of intervening tissue.

sesamoids, one placed laterally and the other posterior to the quadrate. In common with all passerines so far studied, the lower jaw has no medial brace (see Bock, 1960b).

IV. JAW MUSCULATURE

A work of major importance for studies of avian jaw musculature is Lakjer's (1926) review of the trigeminal musculature. For passerines in particular, the paper by Fiedler (1951) provides valuable clarification. Investigations by Bock (1960a and MS) have resolved many remaining problems of structure and terminology within the order, and his nomenclature for the subdivision of complex muscles is the one followed here. The jaw musculature of the Callaeidae remains undescribed beyond the comments of Garrod (1872) and Lowe (1938) on the large size of the 'digastric muscle' (= M. depressor mandibulae).

In describing the structure of complex muscles it is often useful to designate their various aponeuroses by letters or numbers. It is far from clear to what extent these aponeuroses can be homologized between different groups, although the work of Starck and Barnikol (1954) has made progress in this respect for M. adductor mandibulae externus. In the present case, a simple numbering system has been used where necessary, but is not intended to imply homology with any numbered aponeuroses described from other species, with the exception of Aps. 1, 2 and 3 in M. adductor mandibulae externus.

M. adductor mandibulae externus

This important and complex muscle acts to raise the lower jaw and to maintain a grip on objects held in the bill. Its architecture is intricate, and the relationships of its aponeuroses can be better understood by the examination of cross sections (Fig. 18). The abbreviation 'M.a.m.e.' is used in parts of the description to shorten the otherwise unwieldy names of some subdivisions. The three major aponeuroses described by Starck and Barnikol (1954) in a wide range of birds of several orders can be recognized with little difficulty in *Heteralocha*, and their numbering here (Aps. 1, 2 and 3) is the same as Starck and Barnikol's.

M. adductor mandibulae externus rostralis

The most dorsal part of M. adductor mandibulae externus, with an extensive fleshy origin on the cranium. Insertion is made principally via Ap. 1, which narrows anteriorly to form a flat tendon attached to a crista on the surangular. Following Bock, three sections are recognized :

M.a.m.e. rostralis medialis. Origin is from the postero-lateral border of the orbit, medial to the postorbital process, and from a vertically oriented aponeurosis (Ap. 4) attached to the orbit along the medial border of the muscle. Insertion is made via Ap. 1. Medially, a group of fibres from the ventral part of the muscle overlaps part of Ap. 1 as a more or less distinct slip.

M.a.m.e. rostralis temporalis. Origin is fleshy from the border of the temporal fossa ; a short aponeurosis (Ap. 5) runs forwards from the tip of the postorbital

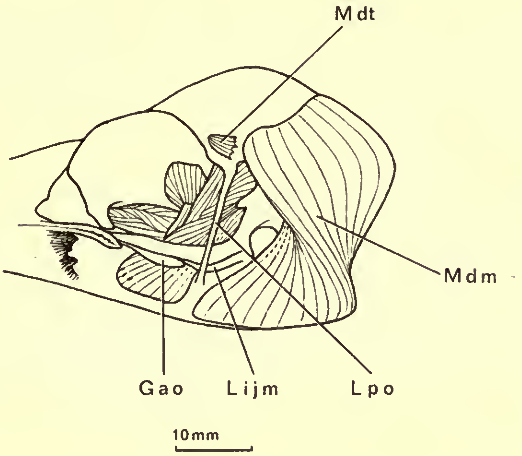

FIG. 11. *Heteralocha acutirostris*, male (♂ 1), jaw muscles and ligaments. For abbreviations see p. 47.

process across the dorsal lateral surface, and in some specimens extends onto the dorsal surface of M.a.m.e. rostralis medialis. The fibres of this section converge anteriorly, falling into an ill-defined bipinnate arrangement, and are attached to the ventro-lateral surface of Ap. 1; a few fibres overlap its dorsal surface posteriorly, but it is exposed for some 8 mm from the insertion.

M.a.m.e. rostralis lateralis. This section lies superficial to the dorsal part of M.a.m.e. ventralis. Its origin is from the lateral edge of the zygomatic process, and from the lateral edge of Ap. 2 in its narrow posterior region. Fibres run upward and medially from the origin and insert on the lateral surface of the mandible over a narrow zone dorsal to the insertion of M.a.m.e. ventralis. This insertion is fleshy, and via a superficial aponeurosis (Ap. 6) which merges medially with Ap. 1. The anterior ventral part of this section lies medial to the jugal bar and is in consequence flattened into a relatively thin sheet of fibres.

M. adductor mandibulae externus ventralis

Origin is from the zygomatic process, by a strong aponeurosis (Ap. 2) which traverses the gap between the cranium and mandible as a fairly narrow tendon, then fans out over the lateral surface of the muscle. Fibres arising from this aponeurosis make an extensive fleshy insertion on the lateral surface of the mandible, spanning the fenestra in the posterior part of the mandible.

M. adductor mandibulae externus caudalis

The shortest section of M. adductor mandibulae externus. Origin is from the otic process of the quadrate and from the ventral surface of the posterior half of Ap. 2. The origin is fleshy, and by a weak aponeurosis (Ap. 7). Insertion is on the dorsal lateral edge of the surangular, posterior and ventral to that of Ap. 1. The insertion is made by a short, narrow aponeurosis (Ap. 3), which bifurcates within the body of the muscle to form a dorsal (Ap. 3a) and a ventral (Ap. 3b) branch. Ap. 7 passes between 3a and 3b before fading out. The muscle shows multipinnate structure, clearest in its middle third, and most conspicuous about Ap. 3a. Fibres run forwards from Ap. 2 to Ap. 3a, back from Ap. 3a to Ap. 7, and forwards again from Ap. 7 to Ap. 3b.

M. pseudotemporalis superficialis

A muscle of relatively simple structure, whose action is adduction of the lower jaw. The origin is a broad fleshy one on the posterior wall of the orbit, immediately medial to M.a.m.e. rostralis medialis. There is also a weak dorsal aponeurosis attached to the orbit. Insertion is made via a strong tendon attached to the medial side of the surangular, ventral to the ramus mandibularis of the trigeminal nerve.

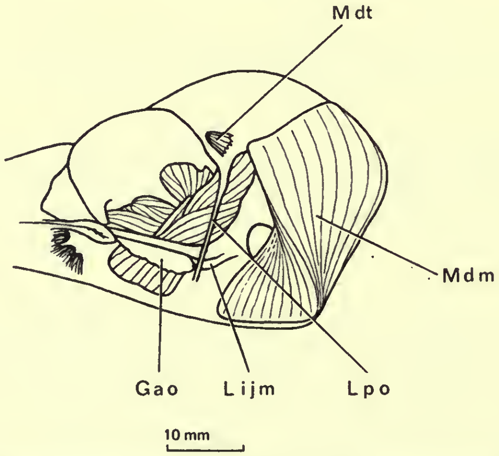

FIG. 12. *Heteralocha acutirostris*, female (♀ C), jaw muscles and ligaments. For abbreviations see p. 47.

M. pseudotemporalis profundus

This muscle is an adductor of the lower jaw, and by its action on the quadrate it also functions to lower the upper jaw. It takes its origin from the dorso-lateral surface of the orbital process of the quadrate, and from a strong aponeurosis attached to the expanded tip of the orbital process. It makes an extensive fleshy insertion on the medial surface of the mandible, overlapping slightly onto its dorsal edge, adjacent to Ap. 1 of M.a.m.e. rostralis.

M. adductor mandibulae posterior

The actions of this muscle are similar to those of M. pseudotemporalis profundus. Due to its situation closer to the mandible-quadrate articulation, it has a lower mechanical advantage, but its upward component may be of value in holding the mandible against the quadrate. M. adductor posterior is contiguous with M.

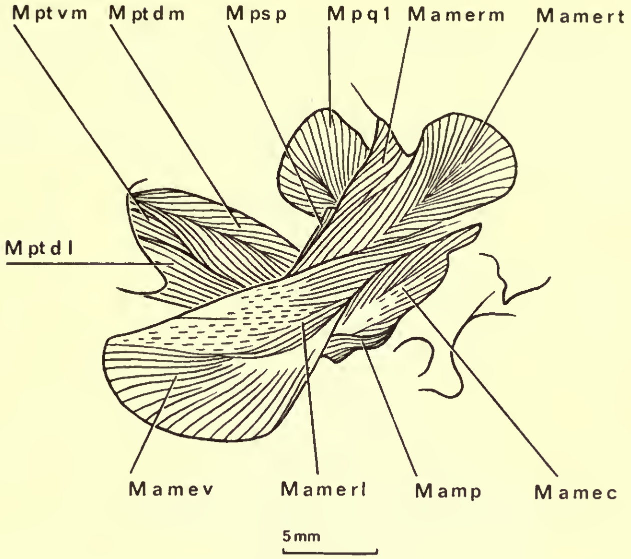

FIG. 13. *Heteralocha acutirostris* (♂ 1), jaw muscles in lateral view. For abbreviations see p. 47.

pseudotemporalis profundus at its origin, which is also a fleshy one on the quadrate, occupying the base of the orbital process and the dorsal surface of the quadrate body. The two muscles are separated (following the criterion used by Lakjer, 1926) by N. pterygoideus. The muscle inserts on the expanded region of the dorsal surface of the mandible just anterior to the base of the internal process, and posterior to the insertion of M.a.m.e. caudalis. The insertion is fleshy and via a weak dorsal aponeurosis.

M. pterygoideus

This important muscle complex acts both to lower the upper jaw and to raise the lower. Its attachments to the palatine and pterygoid are arbitrarily regarded as the origin, and attachment to the lower jaw as the insertion.

M. pterygoideus dorsalis lateralis

This section has an extensive fleshy origin on the dorsal surface of the palatine. It inserts on the medial surface of the mandible, posterior to M. pseudotemporalis profundus, fleshily, and by a superficial aponeurosis (Ap. 1), which is strongest ventrally.

M. pterygoideus ventralis lateralis

Origin is from an aponeurosis (Ap. 2) which is attached to the postero-lateral tip of the palatine, and extends for some distance across the ventral surface of the muscle. The medial edge of this aponeurosis serves to demarcate it from M. pterygoideus ventralis medialis seen in ventral view. M. pterygoideus ventralis lateralis is attached at the base of the internal process of the mandible, ventral to the insertion of M. pterygoideus dorsalis lateralis. There is no overlap ('venter externus') onto the ventral edge or lateral surface of the mandible as in many birds, since the ventral medial edge of the mandible in this region is occupied by a forward extension of M. depressor mandibulae.

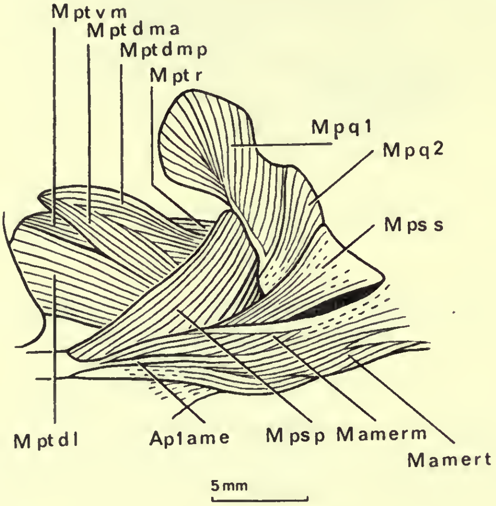

FIG. 14. *Heteralocha acutirostris* (♂ 1), jaw muscles in dorsal view. For abbreviations see p. 47.

M. pterygoideus dorsalis medialis

In dorsal view, this muscle is seen to lie immediately adjacent and posterior to M. pterygoideus dorsalis lateralis, separated from it by a narrow groove which widens medially, exposing a small area of the dorsal surface of M. pterygoideus ventralis medialis. Its origin is confined to the pterygoid, and occupies much of its surface. The muscle falls into anterior and posterior portions, whose fibres diverge in a posterior direction roughly along the lines of the pterygoid, so that it appears bipinnate in dorsal view.

M. pterygoideus dorsalis medialis anterior originates more laterally on the pterygoid, and inserts narrowly on the mandible, immediately caudal to M. pterygoideus dorsalis lateralis. The insertion is fleshy and aponeurotic, the aponeurosis (Ap. 3) being strongest ventrally.

M. pterygoideus dorsalis medialis posterior originates medially on the pterygoid, and fans out to a wide fleshy insertion on the dorsal part of the internal process of the mandible, dorsal to that of M. pterygoideus ventralis medialis.

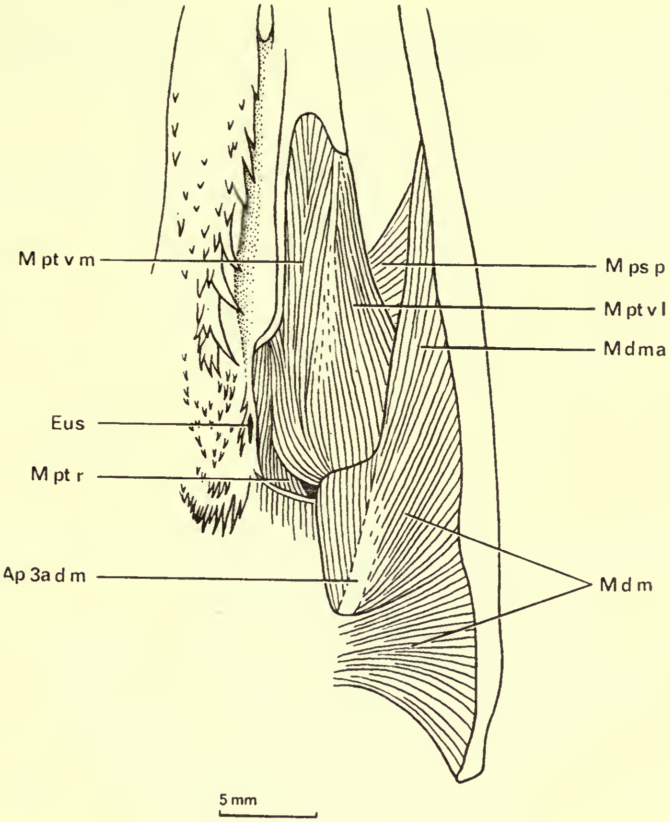

FIG. 15. *Heteralocha acutirostris* (♂ 1). M. pterygoideus and M. depressor in ventral view. Left side of palate left intact to show papillae. For abbreviations see p. 47.

M. pterygoideus ventralis medialis

There is an extensive fleshy origin on the ventral surface of the palatine and insertion is made on the internal process of the mandible, fleshily, and by a strong dorsal aponeurosis (Ap. 4). The fibres of this section are orientated more nearly parallel to the skull axis than those of any other part of M. pterygoideus. On the medial side of the muscle is a slip (M. pterygoideus retractor) exclusively specialized for retracting the palatal apparatus, attached at one end to the medial caudal tip of the palatine, and at the other to the basitemporal plate of the skull. A few of its most medial fibres are attached to the edges of the opening of the Eustachian tube.

M. protractor quadrati et pterygoidei

This muscle acts to raise the upper jaw by moving the palatal framework and jugals forwards. It has a wide fleshy origin from the posterior part of the interorbital septum and the adjacent region of the posterior orbital wall. The lateral border of the muscle lies immediately adjacent to M. pseudotemporalis superficialis.

Two parts can be distinguished. The more anterior and medial part (M. protractor 1), arising mainly on the interorbital septum, shows a bipinnate fibre arrangement. Its raphe is a strong aponeurosis attached to a spur on the posterior dorsal tip of the pterygoid, immediately adjacent to the quadrate. This raphe serves as the principal site of insertion for the fibres of M. protractor 1.

The lateral part (M. protractor 2) originating from the posterior wall of the orbit inserts fleshily, and by a weak dorsal aponeurosis on the caudal edge of the basal half of the orbital process.

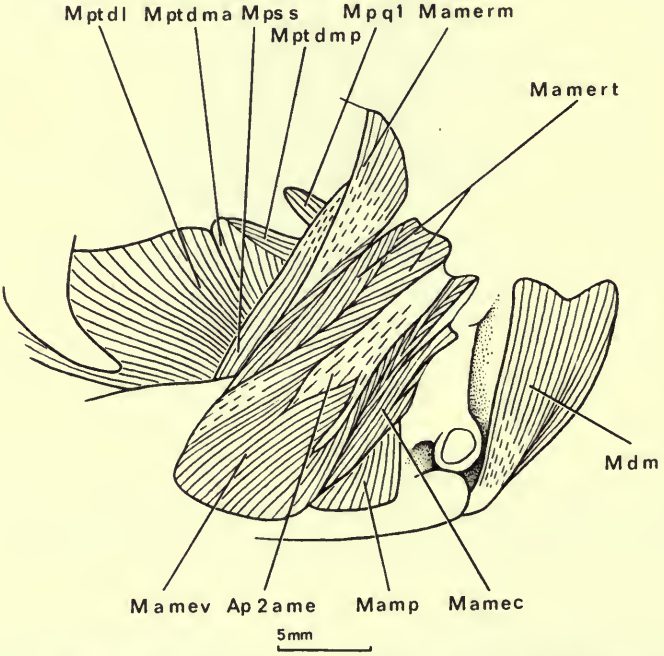

FIG. 16. *Callaeas cinerea,* jaw muscles in lateral view. For abbreviations see p. 47.

M. depressor mandibulae

This muscle, which depresses the lower jaw, is of enormous bulk (and, presumably, fibre number) in *Heteralocha* relative to the other jaw muscles. There is a wide fleshy origin on the squamosal, parietal and exoccipital. Fibres originating high on the cranium converge to insert fleshily near the extremity of the long retroarticular process, mainly on its medial side. Those originating lower, on the exoccipital, fan out to insert fleshily on both surfaces of the retroarticular process. Fibres inserting medially extend far forward beyond the retroarticular process along the ventral half of the mandible, ventral to the insertion of M. pseudotemporalis profundus. This extension is here termed the pars anterior of M. depressor mandibulae.

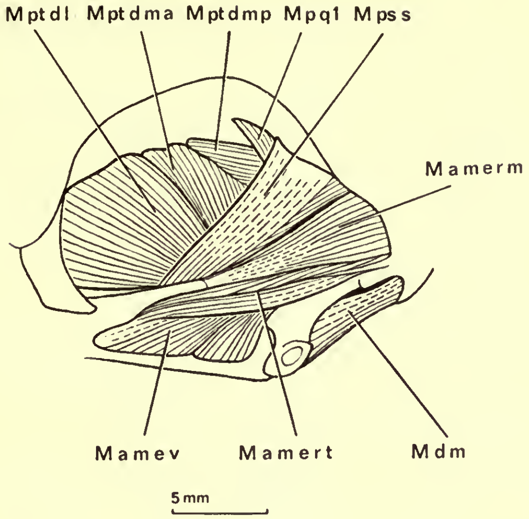

FIG. 17. *Callaeas cinerea,* jaw muscles in dorsal view. For abbreviations see p. 47. M. pseudotemporalis profundus is concealed by M. pseudotemporalis superficialis.

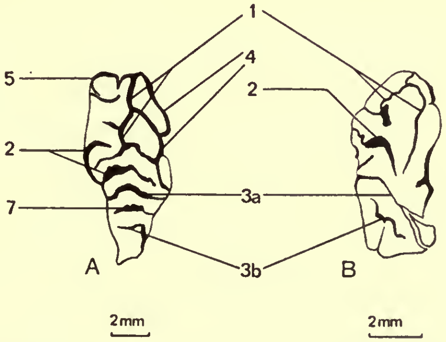

FIG. 18. M. adductor mandibulae externus, TS at about the midpoint of the otic process of the quadrate, and at right angles to it. Numbering of aponeuroses as explained in text. A – *Callaeas cinerea.* B – *Heteralocha acutirostris* (♂ 1). The left side is lateral in both diagrams.

The following aponeuroses can be distinguished :

Ap. 1. This is attached to the cranium around the dorsal edge of the origin on the squamosal and parietal, and extends some way across the lateral surface of the muscle.

Ap. 2. A strong aponeurosis with a narrow attachment at about the middle of the posterior border of the auditory meatus, fanning out across the lateral surface of the muscle, and acting as a surface of origin for fibres inserting on the anterior half of the lateral surface of the retroarticular process.

Ap. 3. A strong aponeurosis attached to the occipital crest, which marks the postero-ventral limit of the origin. Ap. 3 extends some way across the medial surface of the muscle, and becomes stronger on the exoccipital process, whence it is produced as a strong raphe (Ap. 3a) across the ventral region of the muscle, and on into the pars anterior. Fibres arising from its medial side insert mainly on the medial surface of the internal process of the mandible. Those running from its lateral side insert on the medial surface of the basal half of the long retroarticular process, on the posterior face of the internal process at its base, and on the ventral medial surface of the mandible.

Ap. 4. An aponeurosis attached to the dorsal edge of the internal process of the mandible, extending across much of the dorsal surface of the short part of the muscle between this and the exoccipital. This aponeurosis is branched and infolded within the muscle.

Ap. 5. An aponeurosis attached to the dorsal edge of the retroarticular process, but concealed from lateral view by the thin sheet of fibres originating from Ap. 2, and inserted on the lateral surface of the process.

V. BUCCAL CAVITY AND GLANDS

Backwardly directed horny papillae are abundant on the surface of the palate. They are longest where they fringe the choanae, and in a densely clustered transverse row posterior to the internal opening of the Eustachian tubes. The surface of the larynx is also papillate, the papillae being longest at its posterior margin.

Three pairs of salivary glands are present. The Gl. angularis oris lies on the side of the head immediately below the skin and just ventral to the jugal bar ; its duct opens at the angle of the gape. A second gland, which may be termed a Gl. palatinae (see Antony, 1920), lies between M. depressor mandibulae, pars anterior, and M. pterygoideus ventralis lateralis, immediately below the mucosa of the palate. The third gland is a sublingual one. It lies immediately lateral to M. genioglossus, and extends from the level of the anterior border of M. mylohyoideus to the region of the tongue base. Its duct runs alongside M. genioglossus, but diverges from it near the mandibular symphysis to open in a lateral position.

VI. TONGUE APPARATUS

The tongue is narrow, tapering evenly towards its anterior tip which is somewhat frayed and brush like (Fig. 19). The lateral edge bears a few papillae posteriorly, and the posterior edge is crowded with pointed papillae, longest laterally. Tongue length for the specimens examined is shown in Table 1.

The tongue skeleton is similar to that of many passerines. The paraglossalia which provide support for the tongue itself have long posterior processes, and anteriorly they meet and run side by side to a point about one-third of the way from the tip of the tongue. The remainder of the tongue is purely corneous. The basihyal

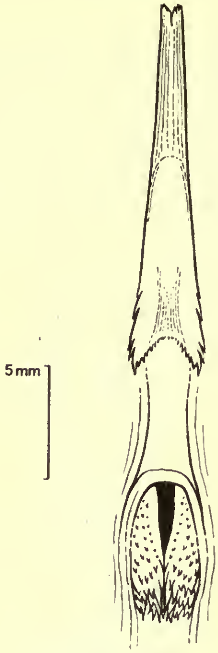

FIG. 19. *Heteralocha acutirostris* (♂ 1), tongue and larynx in dorsal view.

is a slender rod of roughly triangular section, with the apex of the triangle uppermost. The flattened urohyal, expanded at its posterior tip, and the hyoid horns (each consisting of the ceratobranchial posteriorly and epibranchial distally) are of similar form to those of many passerines.

The tongue muscles in *Heteralocha* show few unusual features, and no significant sexual dimorphism was encountered in the dissections. The descriptions given are therefore brief ones ; illustrations are given in Figs. 21 and 22. More detailed accounts and background information are given in the general review by George and Berger (1966) and the paper on passerine tongue muscles by Engels (1938). A very full description of the tongue muscles of a single passerine species is that by Bock (1972) for the extinct *Ciridops anna* (Drepanididae). For discussions on function, reference may also be made to the account of wader tongue muscles by Burton (1974).

M. mylohyoideus

A thin muscular sheet with a long narrow origin on the medial side of the mandibular ramus, inserting on a median raphe. M. mylohyoideus lies ventral to the tongue and all the muscles attached to it.

M. serpihyoideus

Origin is on the occipital plate, medial to the exoccipital process (Bock, 1960b, p. 38) and insertion is on a median raphe continuous with that of M. mylohyoideus.

M. genioglossus

A narrow, strap-like muscle whose origin is from the posterior edge of the mandibular symphysis. The left and right muscles lie side by side near the origin and then diverge, running along the ventral side of the mucosa of the floor of the buccal cavity, on either side of the position of the tongue. In the region of the basihyal, the fibres of the muscle fan out to insert on the connective tissue and mucosa overlying the basihyal and its musculature, and, anteriorly, on the posterior process of the paraglossa.

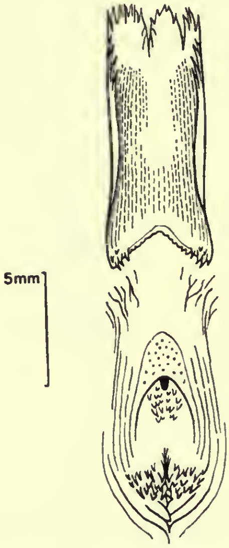

FIG. 20. *Callaeas cinerea*, tongue and larynx in dorsal view.

M. stylohyoideus

A long, narrow muscle originating on the ventral edge of the base of the retroarticular process, and running along the anterior edge of M. serpihyoideus, to insert on the lateral surface of the basihyal, just anterior to M. thyreohyoideus.

M. branchiomandibularis (= M. geniohyoideus of many authors)

A bulky muscle whose origin is on the medial surface of the mandible, ventral to that of *M. mylohyoideus*. A broad anterior and narrow posterior position can be distinguished. The two run parallel to insert on the hyoid horn. The anterior portion meets the horn from the ventral side, and is twisted around it for some distance before inserting on the epibranchial. The posterior portion meets the anterior on the dorso-medial side, and merges with it.

M. ceratohyoideus

A thin, weakly developed muscle which was found only in ♂ 1. It originates on the hyoid horn, on the ventral lateral surface of the distal tip of the ceratobranchial,

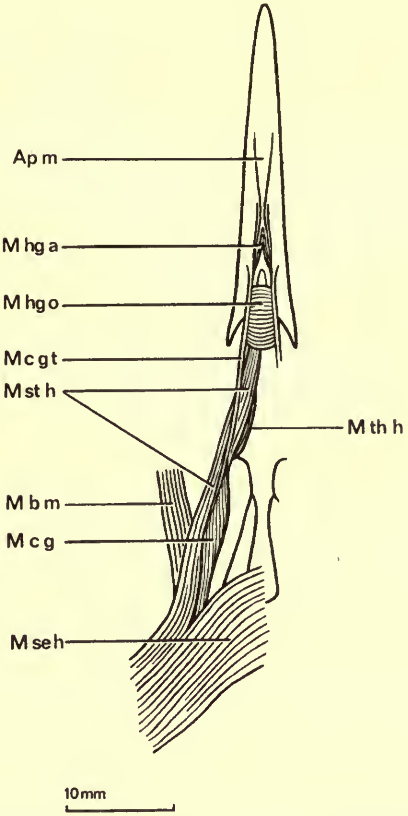

FIG. 21. *Heteralocha acutirostris* (♀ B), tongue muscles in ventral view. For abbreviations see p. 47.

deep to M. ceratoglossus. The insertion is on a median raphe continuous with that of M. serpihyoideus and M. mylohyoideus, near the posterior end of the urohyal.

M. ceratoglossus

A unipinnate muscle whose fibres arise on the surface of the ceratobranchial, and the anterior end of the epibranchial, and insert on a long lateral tendon which is itself inserted on the ventral surface of the paraglossal, just level with the anterior tip of the basihyal. No fibres insert on the tendon over the region lying alongside the basihyal, but just anterior to its attachment to the paraglossal, a small fleshy slip arises. It merges with that from the other side, and together they insert on a strong medial aponeurosis which runs along the ventral side of the paraglossalia, and inserts on the corneous anterior part of the tongue. This slip is referred to by Bock (1972 and MS) as M. hypoglossus anterior. A similar slip in shorebirds was described by Burton (1974) as M. ceratoglossus anterior ; the term 'M. hypoglossus anterior' is used by Burton (1974) to refer to a quite distinct muscle, apparently absent from passerines, arising on the posterior tip of the paraglossals and also inserting on the median aponeurosis.

M. hypoglossus obliquus

Origin is on the postero-lateral process of the paraglossa. The right and left muscles are merged, the whole forming a bulky loop passing ventral to the anterior third of the basihyal.

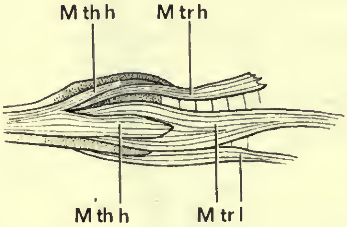

FIG. 22. *Heteralocha acutirostris* (♀ C), ventro-lateral view of tongue muscles attached to the cricoid cartilage. Cricoid and urohyal shown stippled. Both left and right Mm. tracheolateralis are visible. For abbreviations see p. 47.

M. tracheohyoideus

Origin is from the skin of the neck, and insertion on the lateral surface of the cricoid, just below the dorsal origin of M. thyreohyoideus.

M. tracheolateralis

The muscle originates on the syrinx, and passes along the side of the trachea, broadening anteriorly to insert by two heads on the lateral surface of the cricoid.

M. thyreohyoideus

This muscle originates from the lateral surface of the cricoid, by a dorsal and a ventral slip. The dorsal one is slender, and is attached just below the dorsal edge of the cricoid. The ventral slip is broader, and arises between the two heads of insertion of M. tracheolateralis. These slips unite anterior to the larynx and insert on the anterior lateral surface of the basihyal posterior to the insertion of the more slender M. stylohyoideus.

M. ceratoglossus superior (Bock, 1972) was not found in *Heteralocha*. The glottal muscles (M. thyreoarytenoideus and M. constrictor glottidis) conform to Bock's description for *Ciridops anna*.

VII. NECK AND NECK MUSCULATURE

The thorough review by Boas (1929) has provided the basis for most subsequent studies of the avian neck and its musculature. Boas concentrated on non-passerines, principally large species, but detailed information on several small passerines is given by Palmgren (1949). There is, however, little information on the cervical

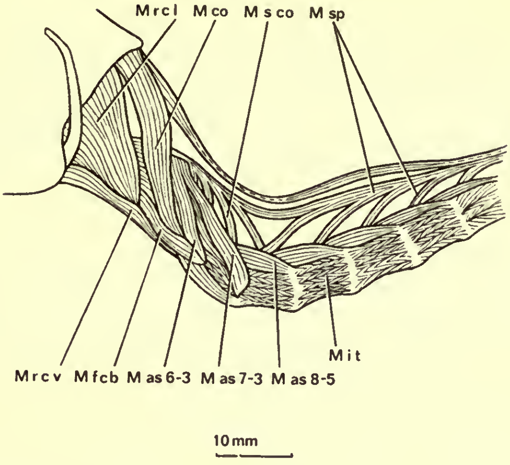

FIG. 23. *Heteralocha acutirostris* (♀ C), lateral view of superficial neck muscles. For abbreviations see p. 47.

muscles of larger passerines comparable in size with the Callaeidae. The majority of neck muscles perform several actions which interact in a complex way, and their individual functions are omitted from the present account in the interest of brevity. Reference may be made to Boas and Palmgren, and to the excellent discussions on neck muscle function by Zusi (1962, 1969).

There are 14 cervical vertebrae in *Heteralocha*, as in most passerines. This total includes the two cervico-dorsal vertebrae (13 and 14) which bear movable ribs not articulating with the sternum, but from a functional standpoint are best treated with the neck. The rib on 13 is extremely short, while that on 14 is long, almost reaching the sternum, but lacking an uncinate process. Six pairs of ribs actually articulate with the sternum, as in *Corcorax*, but unlike most passerines which only have 5 ribs attached to the sternum (Beddard, 1898).

Boas showed that the neck of birds consists of three sections, distinguishable by both functional and morphological differences. Section I, the most anterior, can only be flexed downward, and Section II only upward. Section III can be flexed downward, and also upward at its anterior end. In *Heteralocha*, the constitution of the segments agrees with Palmgren's division for smaller passerines (although Palmgren omitted the cervico-dorsal vertebrae from his count). The division is as follows: Section I, vertebrae 1 to 4; Section II, vertebrae 5 to 9; Section III, vertebrae 10 to 14. The vertebrae of Section I (except the atlas) have strong neural spines and hypapophyses. Those in Section II lack neural spines (except for a weak one on 5) and have no hypapophyses; they are more elongated than the vertebrae of Sections I and III. The vertebrae of Section III have hypapophyses; that on 10 is weak, but they increase in size posteriorly. The last, and largest, hypapophysis is on 15, the first dorsal vertebra. Vertebra 14 has a strong neural spine.

The account below follows the same order and terminology as Palmgren, with modification in the case of Mm. splenii accessorii and Mm. intercristales.

M. biventer

This muscle arises from the dorsal surface of the aponeurosis of origin of M. spinalis in the region of 13, and inserts on the dorsomedial edge of the occipital deep to M. complexus. The muscle consists of two fleshy bellies linked by a flat tendon extending approximately from 8 to 5. Little variation was encountered.

M. spinalis

The muscle consists of a series of fleshy slips from the ventral surface of an aponeurosis attached to the neural spines of vertebrae 14 to 18. These insert on the anapophyses of 2 and of 5 or 6 to 13; the most posterior of these is feeble and indistinct in most of the specimens. Variations in the specimens of *Heteralocha* were as follows:

Slips to both 5 and 6 present: ♀ A, ♀ B.
Slip to 6 present, slip to 5 absent: ♂ 1, ♂3, ♀ C.
Slip to 5 present, slip to 6 absent: ♂ 2.

Mm. splenii colli

These muscles are a series of slips arising from the lateral surfaces of the neural spines of 3 or 4 successive vertebrae, and joining the most anterior slip of M. spinalis which inserts on 2. The vertebrae of origin in the *Heteralocha* specimens are:

4 to 7: ♂ 1, ♀'s A, B and C.
4 to 6: ♂ 2, ♂ 3.

Mm. splenii accessorii and Mm. intercristales

In order to clarify the relationships between these two rather similar groups of muscles it seems desirable to deal with them together. The muscles included under these headings in *Heteralocha* are as follows:

a. A muscle running from the anterior surface of the neural spine of 14 to the transverse-oblique crest of 13, and a similar muscle connecting 13 and 12.

b. A series of muscles connecting the transverse-oblique crests of successive vertebrae from 13–12 to 6–5.

c. Muscles arising on the ventro-lateral surfaces of the neural spines of 5 to 3 and inserting on the transverse-oblique crests of 4 to 2.

d. A muscle arising on the dorso-lateral surface of the neural spine of 3 and inserting on the anapophysis of 2, and a similar but weaker muscle arising on the neural spine and medial part of the neural arch of 2 and inserting on the anapophysis of 1. That arising on 3 closely resembles Mm. splenii colli.

e. A narrow, flat slip arising from the ventral part of the neural spine of 5 and inserting on the anapophysis of 3, somewhat resembling Mm. dorsales pygmaei.

According to Palmgren's criteria, groups *a* and *b* only should be regarded as comprising the Mm. intercristales, and groups *c*, *d* and *e* should be treated as Mm. splenii accessorii. (In the small species examined by Palmgren the two muscles running antero-laterally from the neural spine of 3 are inseparable.) However, it would seem more consistent with Boas's work to include group *c* also in Mm. intercristales, and to reserve the term Mm. splenii accessorii for groups *d* and *e*.

No noteworthy variations between individuals were found.

M. splenius capitis

This muscle originates from the neural spine of 2 and inserts on the posterior surface of the skull deep to M. complexus and M. biventer cervicis. No variations in siting were found, and there is little indication of cruciform structure (Burton, 1971a).

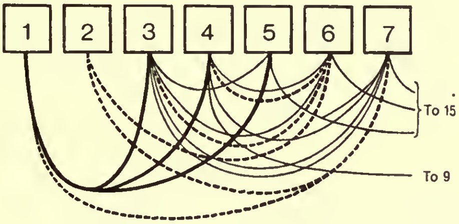

FIG. 24. Diagram to show arrangement of slips of some ventral muscles in the anterior part of the neck in *Heteralocha acutirostris* (♀ B). Heavy lines = M. flexor colli brevis. Broken lines = M. flexor colli profundus. Fine lines = anterior slips of M. longus colli ventralis.

Mm. pygmaei

Origin is from the medial region of the neural arches of 12 to 8. Each muscle inserts on the lateral edges of the transverse-oblique crest of the second vertebra anterior to it except that from 12 which inserts on 11. The latter muscle is weak in most of the specimens and absent in ♂ 1.

Mm. interspinales

These three muscles connect the well-developed neural spines of 2, 3, 4 and 5, and were present in all specimens examined.

Mm. ascendentes cervicis

These muscles arise on the diapophyses of cervical vertebrae up to and including 6. Most consist of two slips inserting on the anapophyses of the second and third vertebrae anterior. That from 7 consists of three slips inserting on 3, 4 and 5 in all specimens, and that from 8 sends an additional slip to 4 in ♂'s 1 and 2. The short slips arising on 12 and posteriorly are relatively weak, and also showed some minor variations in siting. The series is continued posteriorly as Mm. ascendentes thoracicis, but those arising posterior to 14 were not dissected.

Mm. intertransversarii

These laterally situated muscles connect successive vertebrae. The most anterior are those from 3 to 2, and the most posterior those from 13 to 12. Each muscle arises from the anterior surface of the transverse process and inserts on the posterior surface of the transverse process of the vertebra in front; that from 4 to 3 inserts on the medial surface of the rib of 3, and that from 3 to 2 inserts on the lateral surface of the centrum of 2.

As far as 6–5, the Mm. inclusi lie deep to Mm. intertransversarii, and closely associated with them. Palmgren regards the muscles anterior to this as continuing the series of Mm. inclusi ; Boas and Zusi treat them with Mm. intertransversarii as is done here.

The Mm. intertransversarii are multipinnate muscles, traversed by interdigitating raphes from origin and insertion. The muscles are bulkiest and the number of raphes greatest in the region from 7 to 10. Up to 9 raphes have been detected in 9–8 or in 10–9, the number and situation of raphes showing small individual variations. The muscle connecting 13 and 12 is reduced to a small dorsal slip, while those anterior to 5 are also of small size.

Mm. inclusi

These muscles are concealed by Mm. intertransversarii, and can only be separated from them with difficulty. Each one arises on the anterior surface of the transverse process medial to M. intertransversarius, and inserts on the lateral surfaces of the neural arch and centrum of the next vertebra in front. Most show division into dorsal and ventral bellies (Mm. inclusi superiores and inferiores). In the most posterior two (12 to 11 and 11 to 10), only inferiores can be distinguished. The most anterior are those connecting 5 and 6.

M. longus colli ventralis

This complex muscle consists of a series of fleshy slips arising on the sublateral processes, hypapophyses and anterior part of the centra of vertebrae 15 to 6. The main part of the muscle inserts by a series of 7 tendons on the ribs of 11 to 5. Each vertebra sends a slip to join each of the tendons traversing it ; there are thus 7 such slips from each of vertebrae 15 to 12 after which the number of slips decreases by one for each vertebra anterior to this. In the region 15 to 12 the slips are densely crowded and difficult to separate and some of the deepest fibres appear to attach to adjacent vertebrae.

A smaller group of slips situated anteriorly is also included with M. longus colli. Three of these arise from a tendon attached to the sublateral process of 7, which also provides origin for part of M. flexor colli profundus. They insert on ribs 3 and 4 by short aponeuroses and on the long tendon attached to rib 5. Slips also arise on the ventral anterior surfaces of the lateral processes of 7, 6 and 5, the two former in close association with the Mm. intertransversarii, and immediately below them. These attach on rib 3, and those from 6 and 7 also on rib 4 ; minor variations occur. Two slips arise from the sublateral process of 6 and insert on ribs 3 and 4, and there is also a longer slip arising on 9 (8 in ♀ C) which inserts by a weak tendon on rib 4. This tendon also appears to receive some fibres from the posterior part of the muscle.

M. flexor colli brevis

Lateral and medial parts may be distinguished in this muscle. The lateral part constitutes the greater bulk of the muscle and originates from the ventral surface of the lateral strut of 3; and from the lateral processes of 4 and 5 in the ♀'s and 6 also in the ♂'s. The medial portion is separated from the lateral by the anterior part of M. longus colli; it takes origin from the sublateral processes of 3, 4 and 5.

The lateral and medial portions join anterior to rib 3 and insert by a tendon on the postero-ventral processes of the centrum of the atlas.

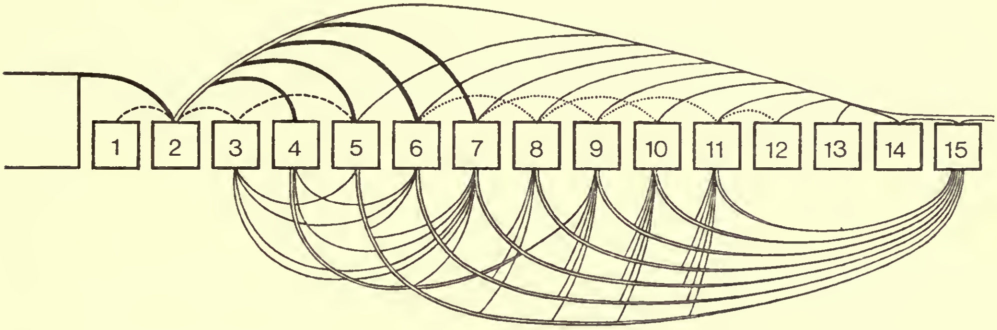

FIG. 25. Diagram to show arrangements of slips of some neck muscles in *Heteralocha acutirostris* (♀ A or ♀ B). Heavy lines = M. splenius capitis and Mm. splenii colli. Fine lines = M. spinalis (dorsal) and M. longus colli ventralis (ventral). Broken lines = Mm. splenii accessorii (as defined in text). Dotted lines = Mm. pygmaei. Tendons of M. spinalis and M. longus colli ventralis are represented by double lines.

M. flexor colli profundus

Origin is from the sublateral processes of 4, 5, 6 and 7. The slips from 4 and 5 arise immediately deep to the medial portion of M. flexor colli brevis and insert on the hypapophysis of 2. From 6, slips run to insert on the hypapophyses of 2, 3 and 4 (♂ 2, ♂ 3, ♀ B) or of 3 and 4 only (♂ 1, ♀ A, ♀ C). From 7 a long slip runs to the hypapophysis of 2; this slip shares a tendinous origin with the medial slip of M. longus colli from 7 to 3. In ♂ 2, ♂ 3 and ♀ B the slip bifurcates and a branch continues forwards to fuse with M. flexor colli brevis near its insertion. The slips arising on 6 show some fusion with M. rectus capitis ventralis at the origin.

M. complexus

Origin is from the lateral strut of 4, the diapophysis of 5, and from an aponeurosis attached to the diapophysis of 6. Insertion is on the dorsal edge of the occipitals.

M. rectus capitis lateralis

Origin is from the hypapophyses of 2, 3 and 4, and insertion on the lateral dorsal edge of the exoccipital.

M. rectus capitis superior

This muscle lies immediately superficial to M. flexor colli brevis. Origin is from the lateral surface of neural arch 1, from the anterior surfaces of anapophyses 2 and

3, from the lateral strut of 4, and from the transverse processes of 5 and 6. Origin from 6 is absent in all the female specimens and in ♂ 2; origin from 5 is also absent in ♀ C. Insertion is aponeurotic and fleshy on a ridge at the posterior edge of the basitemporal plate.

M. rectus capitis ventralis

Origin is from the ventral surface of 1, from the hyapophyses of 2, 3, 4 and 5, and from the sublateral process of 6 where there is some fusion with M. flexor colli profundus. The right and left Mm. recti capiti ventrales are fused in the midline and insert together on the basitemporal plate, anterior to M. rectus capitis superior.

VIII. OTHER CALLAEIDAE

Creadion carunculatus

The description of the Huia's skull by Oliver (in Phillipps, 1963) refers to the general similarity of the skull of *Creadion*. Oliver notes the greater extent of ossification in *Heteralocha*, manifested especially at the front of the orbit. The skull and skeleton of this species are figured by Shufeldt (1913), who includes some brief notes on its skull for comparison with *Anthochaera carunculata* (Meliphagidae).

The following additional points may be noted. The retroarticular process is highly developed in *Creadion*, but is nevertheless relatively shorter than that of the Huia; there is no raised occipital crest, and little development of an exoccipital process. Otherwise, skull proportions are similar to *Heteralocha*, particularly female specimens, though the quadrate and pterygoid are relatively smaller. The skull is apparently larger relative to body size in the Saddleback if a rough index (sternum length) from a single specimen can be relied upon. Ligaments have been removed from the skull of the available specimen, and could not be studied.

With the exception of M. depressor mandibulae, jaw muscles have also been removed from the specimen of *Creadion*. This remaining muscle is, however, of considerable interest, since it possesses a pars anterior as in *Heteralocha* – a feature which otherwise appears to be unique among birds so far studied. The rest of the muscle is also well developed, and similar in structure to that of the Huia, though relatively less massive. The tongue, like the jaws, is smaller relative to the skull in *Creadion*, but the hyoid musculature is closely similar in both Saddleback and Huia.

Due to the historic interest of the specimen, only limited dissection of the neck muscles could be undertaken for *Creadion*. Five of the muscles exhibiting variation in the Huia or among other passerines were examined. These showed an overall reduction in the number of sites of attachment. M. spinalis lacks the slip inserting on 5 which is present in three of the Huia specimens, though a slip to 6 (absent in Huia ♂ 2) is present. M. splenius colli lacks the slip to 7 found in four of the Huia specimens. M. flexor colli brevis and M. rectus capitis superior lack attachment to 6, a feature found in three and two of the male Huia specimens respectively. M. complexus also lacks a slip to 6, although this is present in all six Huias dissected.

Callaeas cinerea

The skull and other features of the skeleton in the Kokako have been described in some detail by Stonor (1942). It is sufficient here to draw attention to the extensive differences in skull proportions and geometry between this bird, on the one hand, and *Heteralocha* and *Creadion*, on the other. The bill is shorter, but much deeper, and the jugal bar meets it at a greater angle. The quadrate is relatively much larger, and is rotated backwards by comparison with the other Callaeidae, so that its otic process meets the lower jaw more nearly at right angles. The cranium is shortened, and smaller relative to the orbits ; the jugal is very long relative to the skull. The lower jaw is deep, and bears strong cristae for the attachment of the adductor musculature. There is no retroarticular process, and the articular is extremely shallow at its articulation with the quadrate. The prominent sesamoids at this articulation were noted by Stonor, and their origin and functions are discussed in detail by Burton (1973). As in the Huia, the external jugomandibular ligament is absent. The occipitomandibular ligament is not ossified at all.

The jaw musculature is notable for the highly developed adductor musculature, and the very small M. depressor by comparison with the other Callaeidae. M. adductor mandibulae externus is considerably more bulky in actual (as well as relative) size than in *Heteralocha*, with increased number of fibres and greater complexity. Its aponeuroses are generally stouter, and more branched and subdivided internally (Fig. 18), providing extra surface for fibre attachment, and consequently a greater use of pinnate structure. M. pseudotemporalis superficialis is also much larger than in the Huia and Saddleback, and in dorsal view completely conceals M. pseudotemporalis profundus, which is much reduced – a consequence of the backward displacement of the quadrate. M. pterygoideus is bulky and the retractor palatini slip is especially well developed, and prominent in dorsal view. M. depressor mandibulae is not only smaller than in the other Callaeidae, but structurally simpler, and entirely lacks a pars anterior. It is unique, however, for the pulley arrangement between its aponeurosis and the internal jugo-mandibular ligament (Burton, 1973).

The tongue is much broader relative to its length than in the Huia and Saddleback ; its shape is almost rectangular, and the tip brush-like. The paraglossa which support it are widely separated. There is no median aponeurosis and M. ceratoglossus anterior is absent ; otherwise, the hyoid musculature resembles that of the other two genera of Callaeidae. The palate is provided with horny papillae similar to those of the other Callaeidae, but the horny lining of both jaws is developed near the bill tip into raised, papillate bosses. There is a pair of Gll. angularis oris, but a Gl. palatinae has not been found.

Neck muscles showing variation in their points of attachment in *Heteralocha* or other passerines were examined in *Callaeas*. The two specimens dissected had the same number and sites of attachment points for the muscles examined. Slips or muscle components absent in some Huia specimens, but present in the Kokako specimens, were the insertions of M. spinalis cervicis on 5 and 6 ; M. splenius colli arising from 7 ; M. intercristalis from 5 to 3 ; the slip of M. ascendens from 8 to 4 ; and the slip of M. flexor colli brevis to 6. No Mm. pygmaei arise from 12, though this site is occupied in all but one male Huia specimen. However, an additional M.

pygmaeus from 7 to 6 is present in the Kokako specimens, though absent in all the Huias dissected. The Kokakos lacked the slip of M. flexor colli profundus from 6 to 2, present in three of the Huias, and the slip of M. complexus to 6, present in all the Huias. M. flexor colli brevis in the *Callaeas* specimens lacks the slip to 6 present in two male Huias, but has a slip to 5 (unlike *Creadion* and one female Huia specimen).

IX. FUNCTIONAL ASPECTS

Jaw mechanism

Next to the form and sexual dimorphism of the bill, the most striking features of the Huia's cranial morphology are the huge M. depressor mandibulae and associated skull modifications – the prominent occipital crest, providing extra surface for its origin, and the very long retroarticular process providing increased leverage for the muscle. Clearly these adaptations must permit the lower jaw to be depressed with great force. This can only be necessary if it is to be opened against considerable resistance by external forces, and it seems certain, therefore, that the Huia was highly specialized for feeding by 'gaping' or 'prying'. This feeding technique consists basically of thrusting the bill into a potentially food-bearing medium (earth, wood, fruit, etc.) and opening it, to widen the hole and so facilitate exploration or prey extraction.

Gaping is a technique described from birds of several families. Among passerines, good examples are furnished by some Sturnidae and many Icteridae. Gaping behaviour and related modifications of M. depressor mandibulae have been studied in the Icteridae by Beecher (1951). It is interesting to compare the Huia with other birds specialized for gaping, and some figures for relative length of the retroarticular process in several examples, mainly of passerines, are given in Table 2. The nearest approach is shown by *Cacicus solitarius* in which the retroarticular process is slightly longer relative to the lower jaw than in the Huia. However, *Cacicus solitarius* is a shorter billed bird ; relative to skull length, its retroarticular process is shorter than in *Heteralocha*, a difference which would be even greater but for the Huia's elongated skull with enlarged occipital crest. It seems clear that the Huia was very highly specialized for feeding by gaping, perhaps more so than any bird now living.

Buller's account of the Huia's feeding behaviour is an excellent one, but clearly gives an incomplete picture of the male's excavation methods. Buller remarks that the captive male used its bill to 'chisel out' pieces of decayed wood in a woodpecker-like manner. Almost certainly its precise technique must usually have been to drive the bill into the wood and 'gape' to split portions off ; this is actually quite different in principle from the methods of woodpeckers which depend purely on blows. Buller states that the female he observed fed in a quite different manner, by probing into relatively hard wood. However, M. depressor mandibulae and the retroarticular process, though somewhat smaller in the female, are still very large by comparison with other birds, and her capacity for forceful depression of the lower jaw must also have been very high. Due to the greater length of the female's bill, less force could be exerted at its tip than in the male ; and the more flexible nature of its anterior, purely rhamphothecal, portion, appears rather inefficient for gaping.

Table 2

Relative length of the retroarticular process in single specimens of various birds showing gaping adaptations, and in all intact Huia specimens used in this study

	A Total length of lower jaw	*B* Length of retroarticular process	*C* Cranium length	*B*/*A* Retroarticular/Lower jaw	*B*/*C* Retroarticular/Cranium
Upupa epops	81·0	5·6	25·4	0·07	0·22
Phoeniculus purpureus	60·4	6·2	26·3	0·10	0·24
Phoeniculus aterrimus	45·4	4·4	20·5	0·10	0·21
Psarocolius decumanus	65·2	7·8	36·9	0·12	0·21
Psarocolius wagleri	72·6	7·9	37·0	0·11	0·21
Cacicus cela	43·1	4·0	29·1	0·09	0·14
Cacicus leucorhamphus	48·7	5·2	29·8	0·11	0·17
Cacicus solitarius	53·5	10·3	31·1	0·19	0·33
Sturnella magna	44·2	5·5	31·3	0·12	0·17
Amblyrhamphus holosericeus	45·4	8·0	28·0	0·18	0·29
Creatophora cinerea	41·7	2·8	28·8	0·07	0·10
Sturnus vulgaris	43·9	5·0	29·4	0·11	0·17
Sturnus contra	49·5	4·7	27·8	0·09	0·17
Heteralocha acutirostris, ♂ (mean of 3)	89·4	16·4	46·8	0·18	0·35
Heteralocha acutirostris, ♀ (mean of 2)	109·5	13·5	43·0	0·12	0·31
Pyrrhocorax pyrrhocorax	77·0	5·4	40·9	0·07	0·13

Nevertheless, gaping must also have been an important part of her repertoire of feeding techniques in addition to exploratory probing (as described by Buller) for which the decurved bill shape is evidently adapted. In probing timber tunnelled by beetles, it seems feasible that the bill might occasionally be inserted through a crack into a larger cavity, so that gaping could take place with contact only in the more rigid basal part of the bill. However, the possibility remains that the female's apparent gaping adaptations reflect principally the shared genotype of the two sexes (see under Sexual Dimorphism).

In addition to its large size, M. depressor mandibulae in the Huia also shows interesting structural complexities. A major contribution to the force of depression is obviously provided by the large mass arising posteriorly and dorsally on the cranium, since this is not only bulky, but has the longest moment arm due to its insertion near the posterior extremity of the retroarticular process. However, the anterior parts of the muscle also exhibit various modifications. Several aponeuroses are present, serving as the basis for pinnate fibre arrangements ; this may be related to their short working distance, for which pinnate structure should provide more forceful contraction than parallel fibred muscles of the same physiological cross section (Gans and Bock, 1965). The pars anterior of the muscle (present also in *Creadion*) is of particular interest, since it appears not to have been described previously in any other bird, and was certainly absent from gaping species of other families dissected during this study. Its functions are hard to surmise, and a satisfactory explanation will probably require a much more detailed knowledge of the jaw mechanics involved in gaping than is available at present.

Except for fibres inserting on the internal process, the greater bulk of M. depressor mandibulae has a medial component in contraction which is greatest for the most posterior parts of the muscle originating near the midline of the cranium. The unusual prominence of the medial condyle of the quadrate may in part serve to resist the stress which this places on the quadrate/mandible articulation.

Probably M. depressor also aids protraction of the upper jaw by the action of its upward force component on the quadrate (see Bock, 1964, 1968, and Zusi, 1962, 1967, for discussions of this mechanism), but M. protractor quadrati et pterygoidei is itself well developed. It is certainly evident that upper jaw action contributes substantially to 'gaping'. The unusual situation of the nasal-frontal hinge may be relevant in this respect. Its position, more dorsal and posterior than in other passerines, places it further from the line of action of the protractor force, acting through the palatines and jugals ; the moment arm of this force is consequently increased.

The remainder of the jaw musculature, concerned with adduction of the lower jaw and depression of the upper jaw, calls for less comment. It is well developed, as seems necessary to provide sufficient grip while extracting huhu grubs, but not remarkably so ; in general features, the muscles other than M. depressor and M. protractor resemble those of *Corvus* described by Bock (MS).

Skull architecture

There is a need for detailed and comparative mechanical analyses of the skull in 'gaping' passerines of a comparable depth to those available for biting and seed crushing forms, e.g. Bock (1960a, 1964b, 1966) and Bowman (1961). Here, some features of possible significance in the skull of *Heteralocha* will be briefly noted.

The wedge-shaped bill of the male Huia is typical of the majority of 'gapers' and resembles that of many Icterids. The straight-sided culmen and gonys are more efficient than the blunter, arched bill of most passerines for the task of forcing the bill into the substrate prior to gaping. Decurved bills, such as those of the female's, or some wood hoopoes (*Rhinopomastus* spp.), depend for this on the presence of existing crevices or tunnels. In the case of the wedge-shaped bill, the narrower and more acutely conical its form, the more easily it will penetrate the substrate ; a limit is imposed by the danger of damage by forces directed across the bill axis, since this hazard is less in a more broadly based cone (see Bowman, 1961, p. 222–224). Evidently this danger was not exceptionally high in the Huia, since the male's bill is narrower and more acute than in many Icterids, including the wood-prying caciques; and in both sexes, the angle between the jugal bars and mandibular rami (giving lateral support to the bill) is no greater than in many unspecialized passerines.

The culmen of the bill and frontal bridge of the skull are virtually in line, again a feature of many 'gapers', but particularly well marked in the Huia, with the nasal-frontal hinge shifted to an unusual position nearly halfway across the orbital region. This profile eliminates the difficulties that might arise with a more conventional skull possessing a marked 'forehead' at the nasal-frontal hinge if the bill were thrust into the feeding substrate up to or past its base. Many Icterids in fact have the culmen raised above the level of the frontal bridge; the horny plate extending onto the forehead of some members of this family (e.g. *Gymnostinops*, *Psarocolius*) is probably adaptive primarily to gaping in succulent fruits (Beecher, 1951).

The stoutness of the quadrate-jugal articulation in *Heteralocha* is probably related to the great development of M. depressor mandibulae. The prominence of the medial condyle of the quadrate and its orientation are also unusual; the long axis of the condyle is directed more nearly at right angles to the skull axis than in most passerines, a feature which may be adaptive to resisting backward disarticulation by strong external forces.

The nasal-frontal hinge appears to be unusually ill defined in *Heteralocha*, and manipulation of skulls relaxed by boiling suggests that the bending zone is considerably longer and stiffer than in most holorhinal birds. This may have some significance as a safety factor, since a wood 'gaper' could be exposed to some danger of over-protraction in the event of timber splitting suddenly while a strong force was still being exerted by the upper jaw. However, there are no bony protraction stops comparable to the overhanging frontal 'brow' of woodpeckers – part of a completely distinct adaptive complex based on the use of M. protractor to distribute compression forces while hammering (Spring, 1965, Bock, 1966).

Buccal cavity, tongue and hyoid musculature

Although the Huia's manner of gaining access to its food is specialized, the food itself (Cerambycid larvae) and the process of swallowing it pose no unusual problems. It is consequently no surprise that the papillae of the upper jaw, tongue and larynx resemble those of many other passerines which feed on invertebrate prey. The hyoid musculature is similarly unspecialized. Cerambycid larvae are smooth skinned, and would not seem to require a great deal of lubrication. The limited complement of salivary glands is consistent with this supposition.

Neck musculature

By comparison with the other two species of Callaeidae, the neck musculature of *Heteralocha* appears better developed inasmuch as several of the muscles or muscle groups occupy additional sites of origin or insertion. It is difficult, however, to draw general inferences from this, owing to the scarcity of information on other passerines. Palmgren's (1949) study, though detailed, concentrated on small species of passerines; Boas (1929) confined his work mainly to non-passerines. In the absence of such information for larger passerines, it is not possible to know to what extent this difference is due to the Huia's larger size. For the present it is only possible to remark that greater development of the neck musculature would be expected in a bird so highly adapted to the extraction of prey from timber by vigorous techniques.

Other Callaeidae

The Saddleback is known to excavate for insect food in decayed timber, bark, epiphytes, etc., and also takes some huhu grubs. It is clear from its skull that in this species, too, gaping must play a large part in its feeding activities. However, it is less specialized than the Huia, even apart from the lack of pronounced sexual dimorphism. Correlated with its smaller body size, it includes a larger proportion of small insects and other items in its diet, and has never reached the high degree of dependence on a single prey species seen in the Huia.

The Kokako is primarily a fruit and leaf eater. In many features of its cranial morphology it shows convergence with finches or with parrots. These features are centred around the need for powerful adduction for biting hard or tough vegetable foods. In the skull, the jaws are shortened and deepened, and the quadrate/mandible articulation shifted posteriorly. The curious structure of the mandible/quadrate articulation is evidently a consequence of these trends (Burton, 1973a). There is no retroarticular process, and it is doubtful if gaping adaptations were ever present in its ancestry. The adductor musculature is more bulky and complex than in the Huia and Saddleback, and the tongue is specialized, probably for dealing with fruits.

X. SEXUAL DIMORPHISM

Bill

The great difference in size and shape of the bill between male and female Huias is of course well known. It does not appear to have been realized, however, to what a large extent this is due to differing development of the rhamphotheca. With the rhamphotheca removed, the bill length difference is reduced and the skulls of the two sexes resemble each other much more closely (Fig. 26). The greatly elongated rhamphotheca of the female is remarkable not only by comparison with the male, but also when compared with other birds of similar bill form. Table 3 gives figures for upper jaw length with and without rhamphotheca in specimens of a variety of birds (mainly passerines) with long decurved bills. It can be seen that all of these fall well short of the female Huia in relative development of the rhamphotheca, and some bills of very extreme form are bony right to the tip. It is difficult to assess the significance of this feature. From a functional viewpoint, it might be suggested that the relatively flexible material of the rhamphotheca would be in less danger of breakage than bone when used for vigorous exploration of timber.

However, developmental and genetic factors should also be taken into consideration. The greater development of the rhamphotheca in the female may be a special case of allometric growth ; this might be investigated by soft x-ray photography of the fairly extensive series of Huia skins in the world's museums. It is also possible

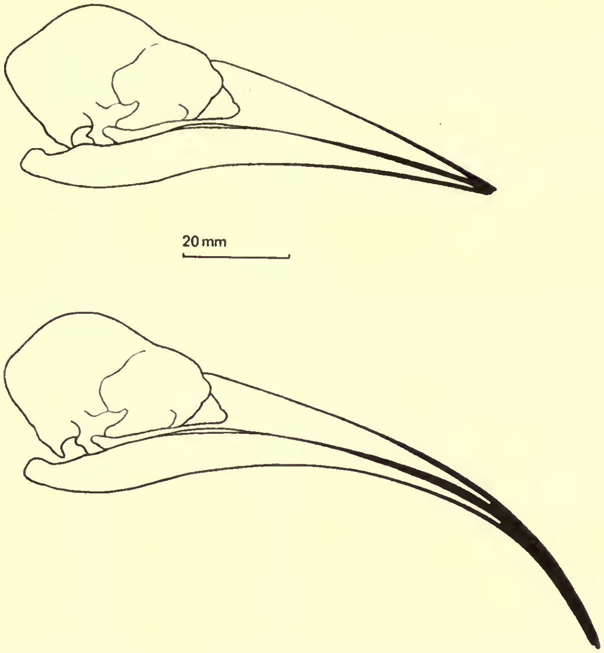

Fig. 26. Comparative development of the rhamphotheca in male and female of *Heteralocha acutirostris* (♂ 1 and ♀ C). Solid black areas represent the profile of the rhamphotheca.

that the answer may lie in the differences between the genetic control of development of rhamphotheca and of bone ; it may simply be 'easier', genetically, to evolve extreme sexual dimorphism of bill length in this way. Other examples of this phenomenon may exist. For example, the lark *Alauda razae* shows marked sexual dimorphism in bill length (Burton, 1971b) and soft x-ray photographs of three specimens of each sex show proportionately greater rhamphothecal development in the longer-billed males. Investigation of longer series of this and other sexually dimorphic species may shed further light on this problem.

Close examination of Huia specimens showing features intermediate between male and female (e.g. some specimens mentioned by Phillipps, 1963) also seems desirable. It may be mentioned in passing that the male specimen figured by Garrod (1872) seems to have been unusual in this respect. Garrod mentions that its tongue was a third the length of the bill. Assuming the tongue was of normal length, this would mean a bill some 90 mm long, a length normally found only in females. The figures show other unusual features ; the jaw tips are attenuated and slightly decurved, rather as in female specimens, and the occipital crest is less prominent than in the males examined in this study. On the other hand, bill depth and stoutness of the jugal, palatines and pterygoids are characteristically male. The specimen was acquired by the Zoological Society of London nearly two years before its death

Table 3

Extension of rhamphotheca beyond upper jaw tip in single specimens of various birds with long downcurved bills, and in male and female Huia specimens used in this study

	A Upper jaw from junction of nasal and jugal bars, rhamphotheca intact	*B* Upper jaw from junction of nasal and jugal bars, rhamphotheca intact	$\frac{A-B}{A}$ Relative length of rhamphothecal extension
Upupa epops	63·5	52·3	0·18
Rhinopomastus cyanomelas	37·7	33·0	0·12
Campylorhamphus trochilirostris	62·0	55·5	0·10
Falculea palliata	66·7	58·5	0·12
Nectarinia famosa	35·2	30·8	0·13
Arachnothera robusta	54·9	53·9	0·02
Hemignathus procerus	60·6	46·8	0·23
Heteralocha acutirostris, ♂ (mean of 3)	50·2	43·5	0·10
Heteralocha acutirostris, ♀ (mean of 2)	90·5	49·7	0·45

(Zoological Society of London, 1870); possibly it was young when acquired, and developed abnormally in captivity.

Jaw mechanism

M. depressor mandibulae is of essentially similar structure in both sexes, but distinctly less massive in the female. Differences in skull features associated with this are the less prominent occipital crest (and consequently shorter skull), and shorter exoccipital and retroarticular processes of the female.

Comparisons between male and female for the other jaw muscles are of very limited value, since these remain in only one female specimen (♀ C). In this specimen, M. adductor mandibulae externus appears distinctly more bulky than in the three males, although the medial slip of M.a.m.e. rostralis medialis is shorter. Greater development of this muscle would seem reasonable in view of the female's greater bill length, a consequence of which would be to reduce the mechanical advantage of the muscle for bill tip adduction – an action which might require considerable force when gripping and extracting huhu grubs.

Skull

Features related to differences in bill form and in development of M. depressor mandibulae have already been mentioned. Apart from these, the proportions of the skull are very similar in both sexes, as can be seen from Table 1. The only significant difference in proportion is in the region of the bill base. In the female, the bill is relatively narrower and less deep at the base, and the skull is narrower anterior to the orbits. Probably her mode of feeling involved less exposure to forces directed across the bill axis than the more vigorous techniques of the male. Ratios of jugal length to sternum length give no indication of any difference between the sexes in relative head size.

Buccal cavity, tongue and tongue musculature

Despite the much greater length of the female's bill, the tongue is of similar size in both sexes. It would have been of little use for the extraction of prey by the female, and in both sexes was probably concerned simply with manœuvring food during the process of swallowing. It is therefore not surprising that the hyoid musculature shows no obvious sign of sexual dimorphism. The same is true also of the buccal papillae and salivary glands, whose functions would have been similar in both sexes.

Neck musculature

Several of the neck muscles and muscle groups showed variations in the number and disposition of components. Table 4 compares the distribution of these variable components in the three spirit specimens of each sex, and a fairly clear pattern emerges. Variable slips and components of the dorsal muscles (concerned mainly

TABLE 4

Distribution of neck muscle components present in some, but not all, of the Huia specimens

	Number of specimens in which present		
	Male	Female	TOTAL
Dorsal components			
M. spinalis insertion on 5	1	2	3
M. spinalis insertion on 6	2	3	5
M. splenius colli origin on 7	1	3	4
M. pygmaeus from 12 to 11	2	3	5
M. ascendens from 8 to 4	2	0	2
TOTAL	8	11	19
Ventral components			
M. flexor colli profundus from 6 to 2	2	1	3
M. flexor colli profundus slip joining M. flexor colli brevis	2	1	3
M. flexor colli brevis origin from 6	3	0	3
M. rectus capitis superior origin from 5	3	2	5
M. rectus capitis superior origin from 6	2	0	2
TOTAL	12	4	16

with raising the neck) are slightly better represented in the female specimens. However, a much greater disparity exists among the variable components of the ventral muscles (concerned with lowering the head and neck), which are much better represented in the male specimens.

This discrepancy is entirely consistent with the difference between the feeding methods of male and female. Forceful downward movements of head and neck must have been essential to enable the male to insert his bill into timber before 'gaping' to split it ; this would have been much less important in the female who relied on the presence of existing tunnels and crevices into which to insert her bill. The preponderance of variable components of the dorsal musculature in the female is less extreme, but may also correspond to a difference in use. Extracting huhu grubs must have entailed exertion in lifting the head and neck for both sexes ; but this exertion may often have been greater for the female, since a larger proportion of her prey would have to be removed from more or less intact tunnels due to the harder wood in which she fed and her lower capacity for forceful 'gaping'.

XI. CONCLUDING REMARKS

Several studies of the Huia's morphology have been undertaken in attempts to clarify its systematic position. I would be reluctant, however, to draw any conclusions about the Huia's affinities from the results of the present investigation. Most of the foregoing descriptions and discussions have been centred around the extremes of sexual dimorphism and adaptation for gaping shown by the Huia, but neither phenomenon is unique among passerines except in degree. Indeed several of the features to which Garrod (1872) gave greatest weight in allying *Heteralocha* with the Sturnidae were gaping adaptations and the genera of 'Sturnidae' which he examined included several New World forms now assigned to the quite distinct family Icteridae. Firstly, the size of M. depressor mandibulae (the 'digastric' muscle) which impressed Garrod and also Lowe (1938) with its similarity to various Sturnidae is an unsatisfactory character unless considered in conjunction with the structure of the muscle. In this respect, *Heteralocha* and *Creadion* both show a feature which is apparently unique – a pars anterior, extending forwards from the articulation with the quadrate. Secondly, *Callaeas*, an undoubted relative (Stonor, 1942) of these two genera, shows no gaping adaptations, and quite possibly did not evolve from a gaping ancestor. It seems reasonable to suggest that the gaping adaptations of the Huia and Saddleback evolved independently of other families and in isolation, and if this is correct, they are poor evidence for affinity with other gaping forms.

The details revealed by this study do not, either, affect the general conclusion of Selander (1966) that extreme sexual dimorphism in feeding structures is particularly frequent in insular bird species, since it provides a means of utilizing a wider range of food resources in conditions of reduced competition. However, the dimorphism of the bill in the Huia is the most extreme example known of this phenomenon, and it is natural to wonder how such a large difference between the sexes evolved. The gaping adaptations may well have played a crucial part. Gaping is an unusual means of exploiting the food resources of timber, and among passerines in general, probing is a much more common technique. Nevertheless, gaping was almost certainly the primary adaptation in the stock from which the Huia arose. The existence of similar adaptations in both sexes of the Saddleback lends strong support to this presumption. If so, the female Huia's bill form appears to be a secondary adaptation for probing, probably evolved from what was initially a slightly more slender (and very likely shorter) bill than that of the male. An early appearance of a sexual difference in feeding technique would be essential for this to take place. It should be stressed here that Buller's account gives no evidence for cooperation between the two sexes in feeding, although the terms in which it is couched appear to suggest this and have often been interpreted in this way. Almost certainly each simply fed independently in the manner for which it was adapted. The female probably derived occasional benefit from the excavations of the male, but the reasons for the Huia's regular association in pairs may primarily have been social or sexual.

Assuming the Huia to be extinct, a full understanding of the significance of its dimorphism may never be achieved. However, there are still various lines of investigation which might profitably be pursued. Further use could be made of the existing material of *Heteralocha*. In addition to the 119 New Zealand specimens examined by Phillipps (1963), several museums in other parts of the world hold series of skins. Examination of all this scattered material may prove difficult, but it would seem desirable to have the fullest available quantitative data on the extent of dimorphism and of variation within each sex. The data so far available suggest that the female's bill may have been more variable than the male's. If true, this might indicate that females obtained food in a greater variety of situations or by more versatile techniques than males (although Phillipps suggests that the male ate a greater proportion of insects other than huhu grubs). It certainly appears that the pair bond was very strong in the Huia, and that both sexes participated in feeding the young.

Studies of the Saddleback may provide information from which inferences about the Huia's behaviour can be drawn, and investigations on its feeding ecology and functional anatomy are currently in progress (Jenkins, pers. comm.). Finally, studies on other timber-feeding birds may shed further light on the Huia's adaptations. The closest parallels to these appear to be shown not by passerines, but by the Wood Hoopoes (Order Coraciiformes, family Phoeniculidae). Within this family, the genus *Phoeniculus* (particularly *P. aterrimus*) appears to parallel the male Huia, while *Rhinopomastus* spp. resemble the female, both genera showing well-marked gaping adaptations. A study of feeding behaviour and anatomy in this family, as well as being worth while in its own right, would make an interesting comparison with the Huia, in which similar bill forms and feeding methods have evolved in the two sexes of a single species.

Yet, finally, it must be admitted that these indirect methods of investigation are a very poor substitute for observations on the living bird. A study of this species in life might have provided much information of general importance for evolutionary biology, and would certainly have been of intense interest ; its loss is a matter for the greatest regret.

XII. ACKNOWLEDGEMENTS

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KEY TO ABBREVIATIONS IN FIGURES

Ap 1 a m e	Aponeurosis 1, M. adductor mandibulae externus
Ap 2 a m e	Aponeurosis 2, M. adductor mandibulae externus
Ap 3a d m	Aponeurosis 3a, M. depressor mandibulae
Ap m	Median aponeurosis of tongue
C o	Occipital crest
E u s	Opening of Eustachian tube
G a o	Gl. angularis oris
L i j m	Internal jugomandibular ligament
L p o	Postorbital ligament
M a m e c	M. adductor mandibulae externus caudalis
M a m e r l	M. adductor mandibulae externus rostralis lateralis
M a m e r m	M. adductor mandibulae externus rostralis medialis
M a m e r t	M. adductor mandibulae externus rostralis temporalis
M a m e v	M. adductor mandibulae externus ventralis
M a m p	M. adductor mandibulae posterior
M as	M. ascendens cervicis.
M b m	M. branchiomandibularis
M c g	M. ceratoglossus
M c g t	Tendon of M. ceratoglossus
M co	M. complexus
M d m	M. depressor mandibulae
M d m a	M. depressor mandibulae pars anterior
M dt	M. dermotemporalis
M f c b	M. flexor colli brevis
M hg a	M. hypoglossus anterior
M hg o	M. hypoglossus obliquus
M i t	M. intertransversarius
M p q 1	M. protractor quadrati et pterygoidei 1
M p q 2	M. protractor quadrati et pterygoidei 2
M ps p	M. pseudotemporalis profundus

M ps s	M. pseudotemporalis superficialis
M pt d l	M. pterygoideus dorsalis lateralis
M pt d m a	M. pterygoideus dorsalis medialis anterior
M pt d m p	M. pterygoideus dorsalis medialis posterior
M pt r	M. pterygoideus retractor
M pt v l	M. pterygoideus ventralis lateralis
M pt v m	M. pterygoideus ventralis medialis
M r c l	M. rectus capitis lateralis
M r c v	M. rectus capitis ventralis
M s co	M. splenius colli
M se h	M. serpihyoideus
M sp	M. spinalis
M st h	M. stylohyoideus
M th h	M. thyreohyoideus
M tr h	M. tracheohyoideus
M tr l	M. tracheolateralis
N f h	Nasal-frontal hinge
P ex	Exoccipital process
P i	Internal process of mandible
P r	Retroarticular process of mandible

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A NEW SKINK (REPTILIA: SCINCIDAE: GENUS *EMOIA*) FROM THE NEW HEBRIDES

WITH COMMENTS ON THE STATUS OF *EMOIA SAMOENSIS LOYALTIENSIS* (ROUX)

By LORD MEDWAY

DURING the Royal Society/Percy Sladen expedition to the New Hebrides, 1971, three immature skinks of an undescribed taxon were caught on Aneityum island. Subsequently three further specimens, taken on the same island by Miss Evelyn Cheesman, were found among the collections of the British Museum (Natural History) where they had been catalogued as *Emoia nigra*. Apart from a note that the period of collecting was 1954–55, Miss Cheesman's material lacks field data. It is likely, but not certain, that the skinks were caught near Red Crest, the camp three miles from the coast (at Anelgauhat) at about 1200 ft (366 m) elevation, occupied by Miss Cheesman from mid-March through July 1955 (see Cheesman, 1957 : 312–327). Of this site, Miss Cheesman has written :

'Plenty of lizards darted about all over the clearing on sunny days, overcast days made them inactive and then one found them under logs, in holes, or hollow trees . . . Individuals were inclined to be tame, a smooth blue-grey skink with a green mate would appear whenever I had meals outside on the clearing. She accepted cheese, bread, biscuit, boiled rice and banana but refused cooked taro, beating a retreat as if insulted. To catch lizards was another matter, but I did succeed in getting a good series.'

During the 1971 expedition skinks were also collected on all other islands visited, i.e. in order northwards from Aneityum, Tanna, Erromanga, Efate, Malekula, Malo, Aore and Espiritu Santo. Previous collections from these islands, and from others in the group, have been reported by Boulenger (1887), Roux (1913), Schmidt & Burt (1930), Burt & Burt (1932) and Angel (1935). Additional unpublished material from the New Hebrides, examined in the course of preparation of this note, is preserved in the Muséum National d'Histoire Naturelle, Paris (François collection), the Natur-Museum Senckenberg, Frankfurt a. Main (Bregulla collection), and the British Museum (Natural History) (mainly collected by J. R. Baker and associates or by E. Cheesman). Other than the six examples from Aneityum, no other representatives of the undescribed skink have been found among any collections. Since it is evidently confined to the island of Aneityum, it is appropriate that the new taxon be named :

Emoia aneityumensis n. sp. – the Aneityum skink

HOLOTYPE. BM 1956.1.3.65, adult male, collected by Miss E. Cheesman on Aneityum island, New Hebrides, South West Pacific, 1954–55 ; for likely place and period of collection, see above.

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PARATYPES. BM 1956.1.3.63, adult male, and 1956.1.3.64, subadult female, also collected on Aneityum by Miss Cheesman during 1954–55; BM 1973.1534 (collectors' number RSNH 14–01), juvenile, apparently female, caught on 19 July 1971, BM 1973.1535 (RSNH 18–01), immature female, 21 July 1971, and BM 1973.1536 (RSNH 19–03), juvenile male, 23 July 1971, all taken in disturbed and partially regenerated forest about 1 mile northeast of Anelgauhat, Aneityum, by Lord Medway and A. G. Marshall.

DIAGNOSIS. In size and colour, and in the scalation of the head, similar to *Emoia samoensis* (Duméril & Duméril), differing in the greater number of longitudinal scale rows and the smaller number of subdigital lamellae. Similarly coloured to *Emoia speiseri* (Roux), but again differing in details of scalation, larger as a mature adult, and evidently producing a greater number of eggs at one time.

DESCRIPTION. An *Emoia*, possessing the characters of that genus as defined by Gray (1845 : 95) and elaborated by Smith (1937). On the head, the prefrontals form a short medial suture, thus excluding the nasals from contact with the frontals. The interparietal is a separate shield, not fused to the parietals. The fifth or sixth upper labial is large, underlying the eye.

The coloration of the holotype, after 18 years in alcohol, is dark brown on the upperparts, with a broken row of irregularly shaped black spots or flecks extending as an interrupted dorsolateral line from the ear orifice to the base of the tail, passing above the origins of the hindlimbs. The flanks are brown, barred and flecked by invasions of the buffy white ventral colour. In the three young animals, when freshly caught, the upperparts were grey-brown or olive-brown, marked with a broken row of irregular spots, flecks or blotches of black, intermixed with flecks of *eau-de-nil*, running from the ear to the base of the tail. The flanks were olive-brown, barred and flecked with the colour of the underparts, which were dirty white. The unbroken tail was the same brown as the ground colour of the upperparts, but regenerated portions were a lighter shade of brown, more or less unmarked. The specimen BM 1956.1.3.63 (again, after 18 years in preservative) is uniformly greyish brown above and buff below, without markings; in my opinion, in life it could well have appeared 'smooth blue-grey' (cf. Cheesman 1957 : 325, quoted above).

Details of scalation and measurements are given in Table 1. By comparison, specimens of *Emoia samoensis* (two syntypes nos. 2764 & 7070 in the Paris museum, two from Samoa nos. 4632 & 4633 in the Basel museum, and two from Erromanga nos. 1860.3.18.8 & 1860.3.18.11 in the British Museum) have 32–36 scale rows at mid-body, 44–51 subdigital lamellae under the fourth toe, and measure snout–vent length 92–102 mm, total length 250–290 per cent. Twelve specimens of *Emoia speiseri* from all parts of this species' range in the New Hebrides have 28–34 scale rows at mid-body, 38–48 subdigital lamellae under the fourth toe, and measure 60–72 mm snouth–vent, total length about 270 per cent (cf. Roux, 1913).

The female *E. aneityumensis* BM 1956.1.3.64 has four enlarged ova in the left ovary and at least one in the right, and BM 1973.1535 has four enlarging ova discernible in the right ovary (left ovary not recognized). Of six undoubted female *E. speiseri* examined, two only had enlarging ova; one had a single large follicle in the left ovary only, and the other had one large follicle in each ovary. Among *E. samoensis*, Roux (1913), has reported a gravid female containing four large ova or eggs ('gros œufs').

There is no reason to believe that *E. aneityumensis* is confined to the vicinity of Anelgauhat on Aneityum. Retrospectively I attribute to this species a grey skink judged to be at least the size of the holotype (Table 1), seen (but not caught) climbing the cliff above the sea-shore at Aegiptzav, on the north coast of the island, in July 1971.

TABLE 1

Scale counts and measurements of the type series of *Emoia aneityumensis*

Reg. no. BM	Longitudinal scale rows at mid-body	Lamellae under fourth toe		Snout–vent length (mm)	Total length[1] (as % snout–vent)
		Left	Right		
1956.1.3.65[2]	40	42	42	92	(250)
1956.1.3.63	40	38	38	89	274
1956.1.3.64	40	36	36	83	(240)
1973.1534	42	39	38	49	257
1973.1535	40	41	41	70	(203)
1973.1536	41	38	39	66	(221)

[1] Figures are given in parentheses if the tail showed signs of loss and subsequent regeneration.
[2] Holotype.

DISCUSSION

The genus *Emoia* is represented in the New Hebrides by ten taxa (Medway & Marshall, in prep.), of which *E. sanfordi*, *E. speiseri* and *E. aneityumensis* are endemic to the archipelago. Only *E. aneityumensis* is confined, as far as known, to a single island.

Of the two taxa most closely resembling *E. aneityumensis*, *E. speiseri* is sympatric with it on Aneityum island. Differences between the two, described above, establish that they are distinct species. *E. samoensis*, on the other hand, has been found in the New Hebrides only on Erromanga, some 180 km north-northwest of Aneityum and the next large island but one. The specimens (BM 1860.3.18.8 & 1860.3.18.11) were collected more than a century ago by Mr Cuming (Boulenger, 1887). In 1971 we did not find the species, but our stay on Erromanga was brief and collecting not intensive ; there are no grounds to doubt the record. The third of Cuming's specimens allocated to this species by Boulenger (BM 1860.3.18.12) is in fact *E. sanfordi*, an identification which confirms at least that the collection derived from the New Hebrides.

Samples of *E. samoensis* from all parts of its range, from the Loyalty Islands to Fiji and the Samoan group, provide no evidence of geographical variation. Separation of the Loyalty Islands population, described as a subspecies by Roux (1913), is not justified. The distinguishing character – adult size invariably less than that of examples from neighbouring archipelagoes ('archipels voisins') – was established by comparison with specimens from the New Hebrides (Roux 1913 : 110). This material (in the Basel Museum of Natural History) was re-examined in the course of preparation of this note. All New Hebrides specimens identified by Roux (1913 : 155) as *Lygosoma* (*Emoa*) *samoense*, a synonym of *E. samoensis*, prove to be *E. sanfordi* and thus provide a fallacious basis for comparison. In the scalation of the head, the number of longitudinal scale rows and of subdigital lamellae, specimens from the Loyalty Islands fall within the range of variation of *E. samoensis* from other parts of the South West Pacific.

The absence of demonstrable geographical variation in *E. samoensis* over this wide area makes it unlikely that the species would differentiate markedly between Erromanga and Aneityum islands. *E. samoensis* and *E. aneityumensis* may replace each other ecologically on their respective islands in the New Hebrides, but there are no grounds for treating the two taxa as geographical races of one species. The characters that distinguish *Emoia aneityumensis* set the taxon apart from all other members of the genus, and it must be treated as a distinct species.

ACKNOWLEDGEMENTS

The Royal Society/Percy Sladen expedition was led by Dr K. E. Lee, on whom fell the chief burden of organization and administration. During field work, Dr A. G. Marshall was jointly responsible for the collection and curation of specimens ; we were assisted on Aneityum by Fred Boe, John Wycliffe and Hugo Tamata. The Royal Society subsequently provided a travel grant which enabled me to visit European museums containing collections of New Hebridean vertebrates ; for their kindness in making available specimens in their care and for other acts of hospitality, I am grateful to Professor J. Guibé, Professor U. Rahm and Dr K. Klemmer. All other work for this paper has been carried out at the British Museum (Natural History), and I am particularly grateful to the Curator of Herpetology, Miss A. G. C. Grandison, and staff for the facilities provided. Miss Grandison and Dr Marshall kindly read and criticized this paper in draft.

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SCUTOCYAMUS PARVUS, A NEW GENUS AND SPECIES OF WHALE-LOUSE (AMPHIPODA: CYAMIDAE) ECTOPARASITIC ON THE NORTH ATLANTIC WHITE-BEAKED DOLPHIN

By ROGER J. LINCOLN & D. E. HURLEY

> 'The sea-lowse is an insect that is an enemy of all kinde of Whales, which by biting and tickling it puts into such a rage, that they are forced to run upon the sand, and hasten to dry land: I know nothing concerning the use of these creatures; but I seriously exhort posterity to search out the use of them.'
>
> From: *The Theater of Insects or Lesser Living Creatures* Book II Chapter 38 p. 1126 by Tho. Mouffet, Doctor in Physick, London, 1658.

INTRODUCTION

It is rare to find a new species of cyamid, rarer still to discover a new genus. Since the first figure and description in the scientific literature of a 'Walfisches Lauss' by Martens in 1675, nineteen accepted species of cyamid have been described, only three of these in this century (Leung, 1967). Fifteen species are ascribed to the genus *Cyamus* and one each to *Neocyamus*, *Platycyamus*, *Syncyamus* and *Isocyamus*. Although the last two were established in 1955, only *Syncyamus* is based on a recently described species.

Their rarity is not unexpected. Cyamids are host-specific to cetaceans which are a well-studied and numerically limited group. It is even more surprising, then, to discover in the collections of the British Museum (Natural History), unrecognized since their collection in 1933, specimens of a distinct and new species of cyamid from a common North Atlantic dolphin from which cyamids have never, to our knowledge, been recorded.

These cyamids stood out for two reasons; their generally small size in comparison with other species in the collection, and their distinctively rounded, saucer-shaped, low-profile outline which immediately suggested their novelty. These features indicated that their host would prove to be a fast-swimming species, which is indeed the case, and the subsequent examination has revealed further adaptation to life in an area of turbulent flow in the shape of the dactyls and cramp-iron teeth on the body and appendages.

The cyamids were collected by Dr F. C. Fraser from a white-beaked dolphin, *Lagenorhynchus albirostris* Gray, and later presented to the Crustacea Section. The

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dolphin was caught in the North Sea, off Peterhead in Aberdeenshire, on 21 July 1933. It was a young female measuring 5 ft 7½ in. in length with a pronounced deformity in the curvature of the spine behind the dorsal fin (Fraser, pers. comm.).

SCUTOCYAMUS gen. nov.

DIAGNOSIS. Pereon segments 3–4 and 6–7 fused. Antenna 1, 2-articulate; antenna 2, 1-articulate. Maxilla 2 with outer lobes absent. Maxillipeds fused and markedly reduced to form a small cleft flap. Pereopods 1 and 2 strongly dissimilar in shape and with 1 very much smaller than 2; pereopod 2 only 3-articulate. Male without accessory gills. Type species, *Scutocyamus parvus* sp. nov.

Scutocyamus parvus sp. nov.

(Text figs. 1a–g, 2a–h; Pl. 1a–e)

DIAGNOSIS. With the characters of the genus given above. Body of small size, robust, strongly flattened dorsoventrally, head weakly immersed into anterior pereon segment. Pereopod 1 (Fig. 1c) lacking unguis, dactylus armed with numerous small teeth (Pl. 1e); pereopod 2 and pereopods 5–7 powerfully developed and held in characteristic posture giving a general oval symmetry to the shape of the animal (Fig. 1a; Pl. 1a). Gills simple, single. Pereon segments 5–7 each with a pair of large spines on the ventral surface.

DESCRIPTION. Length of body from apex of head to end of pereon 1·7–2·4 mm in male and 2·6–3·1 mm in ovigerous female. Maximum width of body at the level of tergite 5 from 0·9 to 1·3 mm in male and from 1·4 to 1·8 mm in ovigerous female. No trace of pigmentation remaining in the alcohol preserved material. Pereon (Fig. 1a) somewhat oval in outline (pereon segment 1 fused with head), male rather more slender than female; tergites 3–4 in female slightly shorter than other tergites, in male very much shorter and also much narrower than other tergites (Fig. 1b); tergite 7 weakly immersed into pereon segment 6 (Fig. 1a, b); a pair of strong spines on the ventral side of segments 5–7. Head with sides convex, immersed slightly into anterior pereon segment, anterolateral angles expanded into large lobes giving a wide frontal margin to head; eyes small, oval, mid-dorsal. Antenna 1 (Fig. 2c) small, 2-articulate, article 2 longer than 1, apex with prominent group of sensory setae. Antenna 2 (Fig. 2d) extremely small, 1-articulate, but constriction near tip gives impression of separate terminal article, apex with several large sensory setae. Upper lip (Fig. 2e) large, outer margin weakly concave and densely fringed with fine setae. Mandibles (Fig. 2g) with 2 incisor processes, the anterior of 1–2 teeth, the posterior incisor of several teeth; right mandible with 2 penicils, left with only one; molar process a rounded protuberance covered with very fine setae. Lower lip (Fig. 2f) with inner lobes fused into a single elongate lobe, outer lobes slightly broader than inner, distal margins fringed with long setae. Maxilla 1 (Fig. 2h), apex with 3 pairs of curved spines each with 2–4 small teeth on inner margin; palp 1-articulate, reaching to about the apex of the outer lobe and with

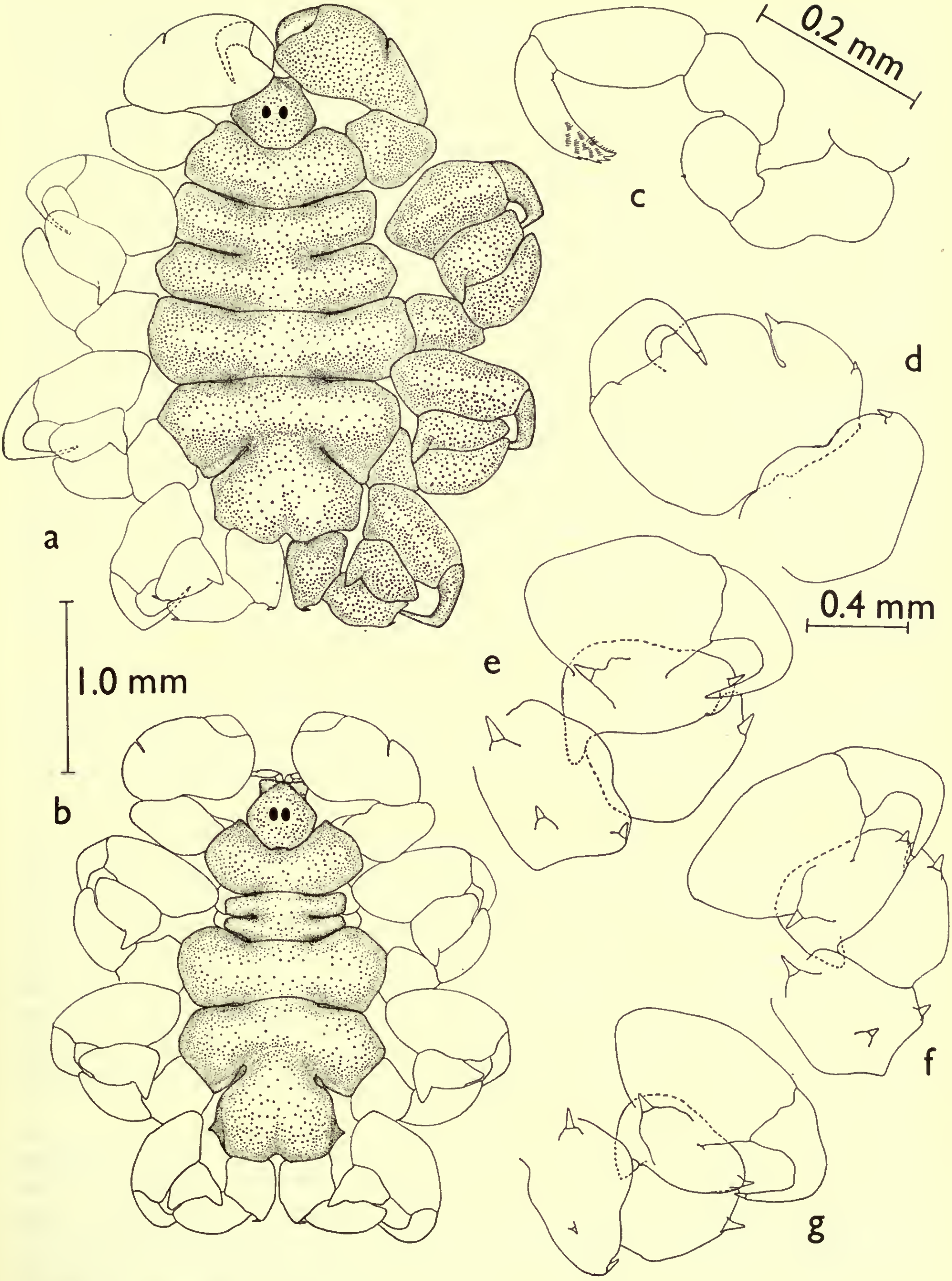

FIG. 1. *Scutocyamus parvus* sp. nov. a, dorsal entire, female ; b, dorsal entire, male ; c, pereopod 1 ; d, pereopod 2, ventral ; e, pereopod 5, ventral ; f, pereopod 6, ventral ; g, pereopod 7, ventral ; bar scale a–b, 1·0 mm ; c, 0·2 mm ; d–g, 0·4 mm.

small group of sensory setae at tip. Maxilla 2 (Fig. 2b) a single elongate lobe with a small group of sensory setae at tip; right and left maxilla 2 fused along mid-line. Maxillipeds (Fig. 2b) fused and reduced to a small cleft flap. Pereopod 1 (Fig. 1c) extremely small, simple, 5-articulate, propodus elongate and about twice as long as wide; dactylus broad with numerous combs of small teeth towards apex (Pl. 1e), unguis absent. Pereopod 2 (Fig. 1d) powerfully developed, only 3-articulate, proximal article large and robust with small marginal spine; article 2 very broad and flattened, the outer margin with a deep indentation which probably marks the point of fusion of two articles; article 2 with 2 small marginal spines; dactylus robust strongly angled at its mid-point, and with a small but sharply pointed unguis. These cyamids have a quite characteristic posture with the expansive second pereopods held across the front of the head to form an effective shield. Pereopods 5–7 (Figs. 1e, f, g) powerful, 5-articulate, basal article (basis + ischium) short and stout with 3 well-developed ventral spines; merus broad and flat with a single spine on distal margin; carpus about equal to size of merus with a small spine on distal margin and an extremely large mid-ventral spine, the inner posterior angle produced into a small triangular process overlapping the dorsal surface of merus; propodus elongate and extremely robust; dactylus acutely angled and with sharply pointed unguis. Gills single, quite short, tapering somewhat, and held across ventral surface of pereon in forward direction; accessory gills absent in male. Brood pouch rounded (Fig. 2a), containing only 7–10 eggs or young; margins of oostegites fringed with many short setae; genital valves well developed with inner margin also fringed with small setae. Pleon a small bilobed structure.

MATERIAL EXAMINED. 11♀♀ (ovigerous), 2·6–3·1 mm length, 1·4–1·8 mm width: 21♀♀ (immature), 2·0–2·5 mm length, 1·1–1·4 mm width: 28♂♂, 1·7–2·4 mm length, 0·9–1·3 mm width: 37 juveniles. Holotype ♀ registration no. 1973 : 105; paratypes registration no. 1973 : 106, deposited in the collections of the British Museum (Natural History).

REMARKS. *Scutocyamus parvus* can be immediately recognized by the small body size, general symmetry given to the body posture by the expansive second pereopods, and by the fusion of pereon tergites 3–4 and tergites 6–7. Only one other species, *Syncyamus pseudorcae* Bowman, has a similar fusion of the pereon segments but it is restricted to tergites 6–7. While the amalgamation of tergites 3–4 is complete in *Scutocyamus* (Pl. 1d) the posterior tergites retain a weak demarcation line which can be mistaken for a suture under a light microscope. Confirmation that pereon tergites 6–7 are in fact fused was obtained by examining material with a scanning electron microscope. The demarcation line was found to be a shallow depression which follows the line of fusion of the two segments.

Of the five recognized genera of cyamids, *Scutocyamus* seems to be most closely allied to the monotypic *Syncyamus*. In addition to the fusion of the pereon tergites both have a similar reduction of the mouthparts, especially the reduction of the maxillipeds to a small flap, the fusion of the second maxillae, and the fusion of the inner lobes of the lower lip. Also, the absence of an unguis on the small pereopod 1 is a character shared by the genera. However, *Scutocyamus* retains a number of

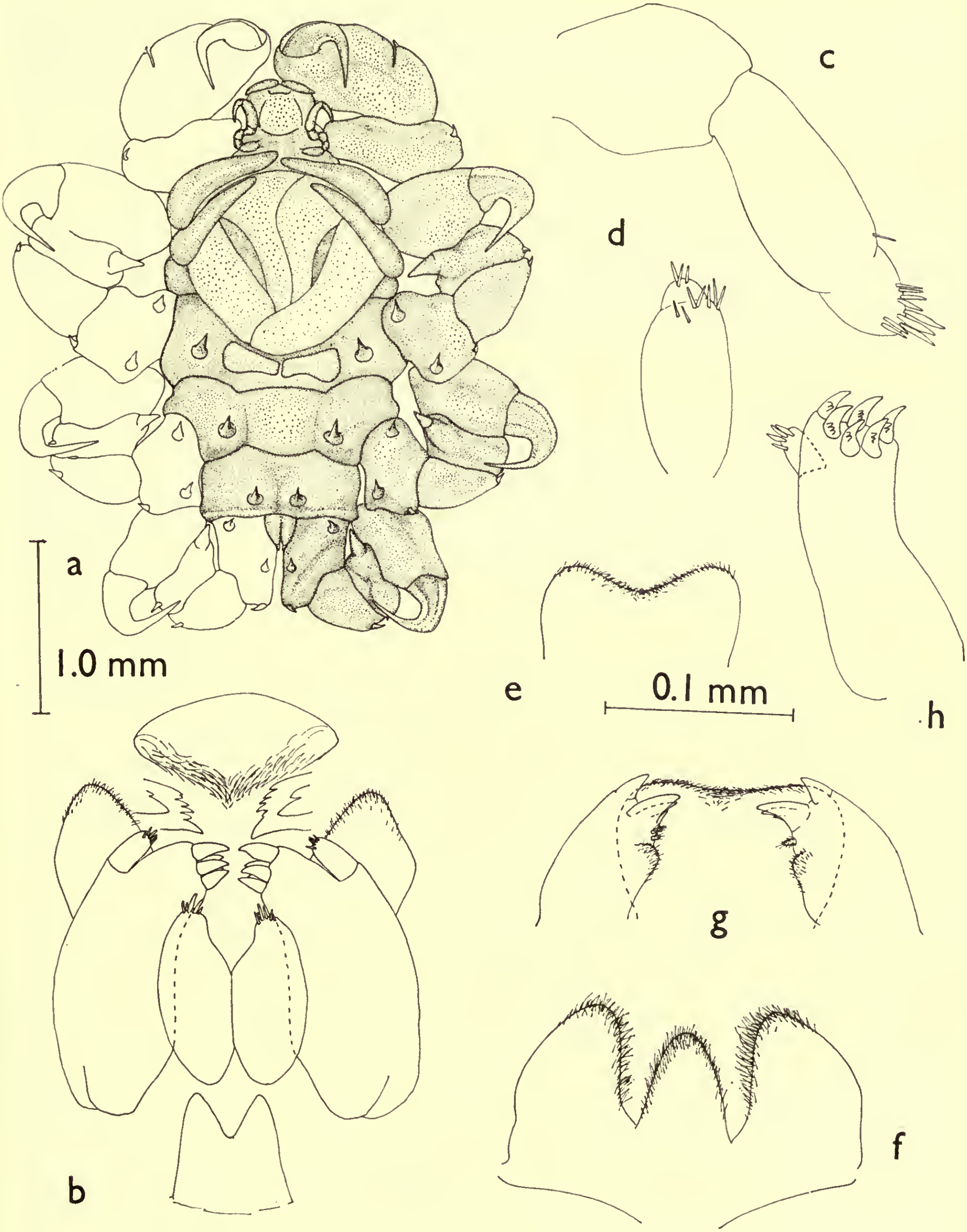

FIG. 2. *Scutocyamus parvus* sp. nov. a, ventral entire, female ; b, mouthparts, ventral ; c, antenna 1 ; d, antenna 2 ; e, upper lip ; f, lowerlip ; g, mandible with upper lip ; h, maxilla 1 ; bar scale a, 1·0 mm ; b–h, 0·1 mm.

unique characters such as the fusion of pereon tergites 3–4, extreme reduction of the antennae and pereopod 1, a 3-articulate pereopod 2, and an absence of accessory gills in the male. The armature of comb-like teeth on the propodus of pereopod 1 has not previously been reported and appears to be an adaption to scrape the surface of the host.

ACKNOWLEDGEMENTS

The authors wish to thank Dr F. C. Fraser for his assistance with original data and for drawing attention to the opening quotation. The junior author wishes to thank the Trustees of the British Museum (Natural History) for facilities made available during Official Leave from New Zealand.

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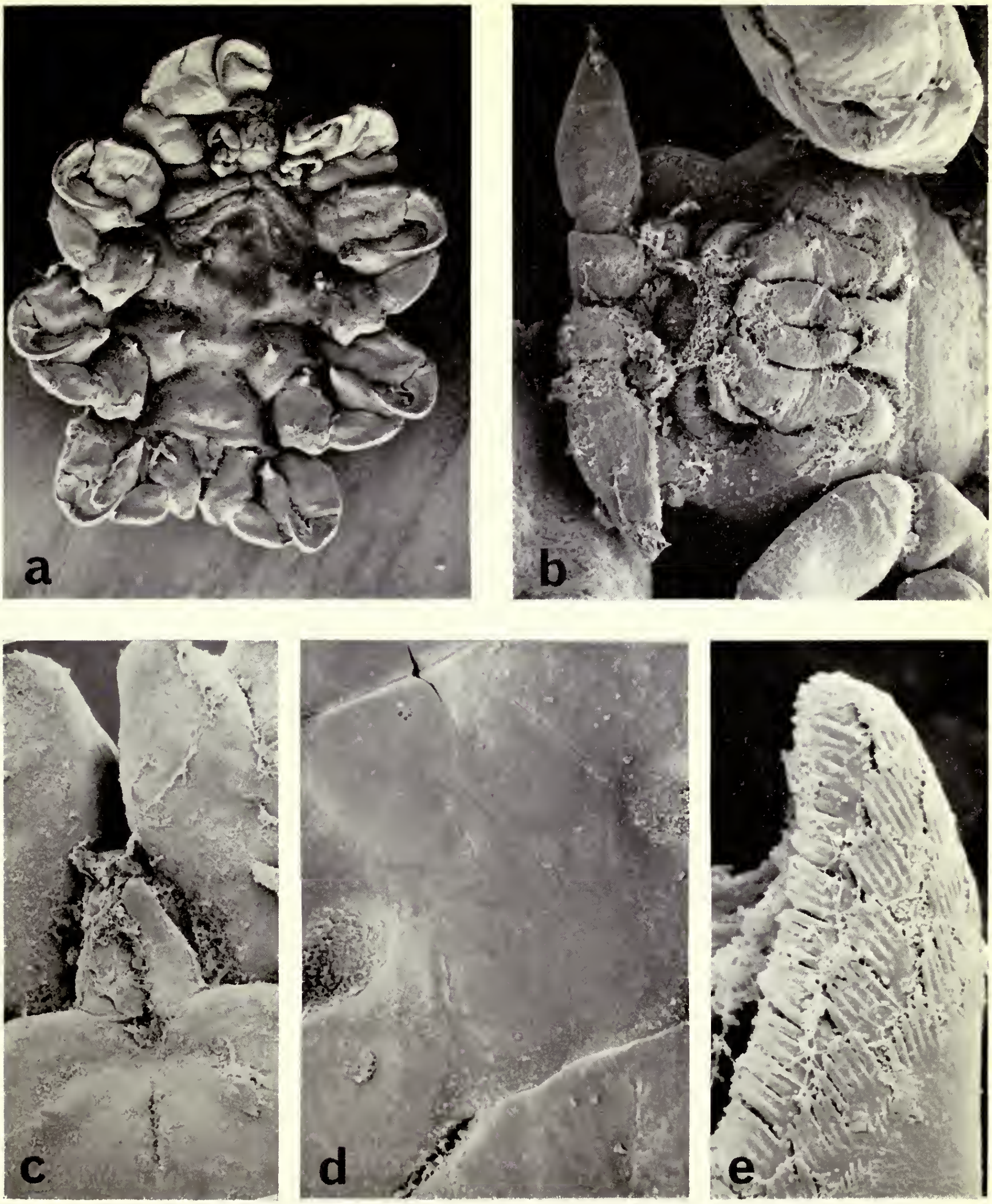
PLATE 1

Scutocyamus parvus sp. nov. a, entire ventral, male (× 30) ; b, mouthparts, male (× 180) ; c, pleon ventral, male (× 120) ; d, fusion pereon tergites 3–4, dorsal female (× 120) ; e, pereopod 1, apex of propodus, male (× 1·1 k). Scanning electron microscope ; gold coating ; 20 kv.

PLATE 1



CATALOGUE OF THE WHALE-LICE (CRUSTACEA : AMPHIPODA : CYAMIDAE) IN THE COLLECTIONS OF THE BRITISH MUSEUM (NATURAL HISTORY)

By ROGER J. LINCOLN & D. E. HURLEY

INTRODUCTION

THE collections of the British Museum (Natural History), containing as they do much of the material taken during the *Discovery* Investigations (1925–27) on the biology of the southern whales and much incidentally collected Northern Hemisphere material, represent one of the more significant collections of cyamid material. Numerically this collection is not large but it contains some types and material which has been little studied. Furthermore the group is usually very poorly represented in museum collections.

The discovery of a new genus and species of cyamid (Lincoln & Hurley, 1974) has been one of the benefits resulting from a re-examination of the material in the collections of the Crustacea Section. Since all identifications have now been verified and labelling updated following the nomenclature given in the recent cyamid synopsis of Leung (1967), this is a suitable opportunity to present a published catalogue of holdings for the benefit of other workers. The nomenclature for the whales follows that used by Hershkovitz (1966).

The assistance of Miss J. Ellis in collating the information is gratefully acknowledged.

CYAMUS Latreille, 1796

Cyamus abbreviatus Say, 1818

(1) Type ? 1 specimen (dry collection). North America. Leach Collection.

Cyamus balaenopterae Barnard, 1931

(1) Syntypes, 6♂♂, 4♀♀ ; *Ann. Mag. nat. Hist.* (10) **7** : 425–430. Reg. no. 1936: 11:2:3495–3501. Saldanha Bay, South Africa ; on *Balaenoptera physalis* (L.) [blue whale according to label] whale no. W 1096. *Discovery* Collection.

(2) 2♂♂, 8♀♀, 1 juv. Reg. no. 1936:11:2:3502–3531. Saldanha Bay, South Africa ; on *Balaenoptera musculus* (L.) whale no. W 867. *Discovery* Collection.

(3) 9♂♂, 6♀♀. Reg. no. 1936:11:2:3502–3531. Durban, South Africa ; on *Balaenoptera physalus* (L.) whale no. W D19. *Discovery* Collection.

(4) 1♂, 5♀♀ (immature). Reg. no. 1936:11:2:3502–3531. Saldanha Bay, South Africa, 18.8.1926 ; on *Balaenoptera musculus* (L.) whale no. W 961. *Discovery* Collection.

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(5) 3♂♂, 6♀♀, 1♀ ovig., 1 juv. Reg. no. 1936:11:2:3502–3531. Saldanha Bay, South Africa, 15.8.1926; on *Balaenoptera physalus* (L.) whale no. W 948. *Discovery* Collection.
(6) 20♂♂, 15♀♀, 10 juvs. Reg. no. 1973:104:45. No locality data, 24.10.1948; on *Balaenoptera physalus* (L.). *Discovery* Collection.

Cyamus boopis Lütken, 1870

(1) 1♂. Reg. no. 1853:68. Greenland. Collected by Holboll.
(2) 10♂♂, 10 juvs. Reg. no. 1910:8:9:1–6. Bransfield Straits, South Shetlands; on *Megaptera novaeangliae* (Borowski). Collected by J. A. Mörch.
(3) 2♂♂, 1♀ (immature). Reg. no. 1911:11:8:23064–066. No locality data. A. M. Norman Collection.
(4) 3♀♀. Reg. no. 1920:7:5:61–62. Deception Island, South Shetlands, 1914; on *Megaptera novaeangliae* (Borowski). Collected by A. G. Bennett.
(5) 11♂♂. Reg. no. 1924:7:10:1–5. Olna Firth, Shetland Islands, 19.6.1924; on *Megaptera novaeangliae* (Borowski). Collected by F. V. Morley.
(6) 3♂♂, 3♀♀ (immature), 2 juvs. Reg. no. 1928:12:1:2966–71. Durban, South Africa, 23.7.1908; on *Megaptera novaeangliae* (Borowski). T. R. R. Stebbing Collection.
(7) 1♂, 2♀♀ (all immature). Reg. no. 1936:11:2:3542–3581. South Georgia; on *Megaptera novaeangliae* (Borowski) whale no. 355. *Discovery* Collection.
(8) 6♂♂, 1♀. Reg. no. 1936:11:2:3542–3581. South Georgia; on *Megaptera novaeangliae* (Borowski), whale no. 373, genital region. *Discovery* Collection.
(9) 2♂♂, 2♀♀, 5 juvs. Reg. no. 1936:11:2:3542–3581. South Georgia; on *Megaptera novaeangliae* (Borowski), whale no. 387. *Discovery* Collection.
(10) 3♂♂, 3♀♀, 10 juvs. Reg. no. 1936:11:2:3542–3581. Deception Island, South Shetlands; on *Megaptera novaeangliae* (Borowski). *Discovery* Collection.
(11) 6♂♂, 4♀♀, 10 juvs. Reg. no. 1936:11:2:3542–3581. Saldanha Bay, South Africa, 29.9.1926; on *Megaptera novaeangliae* (Borowski), whale no. 1125. *Discovery* Collection.
(12) 11♂♂, 1♀. Reg. no. 1936:11:2:3542–3581. Durban, South Africa; on *Megaptera novaeangliae* (Borowski), whale no. D3. *Discovery* Collection.
(13) 2♂♂, 4♀♀. Reg. no. 1936:11:2:3542–3581. Durban, South Africa, on *Physeter catodon* L., whale no. D21. *Discovery* Collection.
(14) 10♂♂, 7♀♀, 2 juvs. Reg. no. 1936:11:2:3542–3581. Saldanha Bay, South Africa, 6.8.1926; on *Megaptera novaeangliae* (Borowski), whale no. 918. *Discovery* Collection.
(15) 16♂♂, 9♀♀, 10 juvs. Reg. no. 1965:9:8:1–15. Paita, Peru, 05°05′ S, 81°10′ W, 19.10.1960, on *Megaptera novaeangliae* (Borowski), ♀ 13·3 m, whale no. PA1. Collected by Robert Clarke.
(16) 2♂♂. Reg. no. 1972:556:2. Varanger Fiord, Norway; on *Megaptera novaeangliae* (Borowski). G. O. Sars Collection.
(17) 50♂♂, 10♀♀ (immature). Reg. no. 1972:568:60. Off Russell Bay, Bay of Islands, New Zealand, August 1912; on *Megaptera novaeangliae* (Borowski). Terra Nova Collection.

(18) 150♂♂♀♀. Reg. no. 1972:569:150. Off Russell Bay, Bay of Islands, New Zealand, August 1912 ; on *Megaptera novaeangliae* (Borowski). Terra Nova Collection.
(19) 14♂♂, 6♀♀. Reg. no. 1972:577:20. No locality data. No collection data.
(20) 9♂♂, 6♀♀ (immature), 1 juv. Reg. no. 1972:579:16. St. Vicente. Collected by R. T. Lowe.

Cyamus catodontis Margolis, 1954

(1) 300♂♂♀♀ (mature and immature). Reg. no. 1965:9:8:16–45. Paita, Peru 05°05′ S, 81°10′ W, 30.9.1960 ; on *Physeter catodon* L., ♂ 13·2 m, whale no· Pa870. Collected by R. Clarke.
(2) 100♂♂♀♀. Reg. no. 1965:9:8:16–45. Pisco, Peru, 13°47′ S, 76°15′ W, 17.10. 1960 ; on *Physeter catodon* L., ♂ 13·6 m, whale no. Pi59. Collected by R. Clarke.
(3) 150♂♂♀♀ (mature and immature). Reg. no. 1965:9:8:16–45. Pisco, Peru, 13°47′ S, 76°15′ W, 17.1.1961 ; on *Physeter catodon* L., ♂ 15·2 m, whale no. Pi160. Collected by R. Clarke.
(4) 150♂♂, 150♀♀. Reg. no. 1973:103:300. No locality data ; on *Physeter catodon* L., ♂ 54 ft, whale no. 20. *Discovery* Collection, 1951–52.

Cyamus ceti (L., 1758) Lamark, 1801

(1) 1♂, 1♀. Reg. no. 1911:11:8:23075–75. No locality data ; A. M. Norman Collection.
(2) 3♂♂, 8♀♀. Reg. no. 1928:12:1:2978–2984. Greenland ; on *Balaena mysticetus* L. T. R. R. Stebbing Collection.
(3) 6♂♂, 3♀♀. Reg. no. 1956:10:10:340–343. Arctic Sea, 1893. University College, Dundee Collection (S.S. *Eclipse*).
(4) 300♂♂, 200♀♀, 50♀♀ (immature), 50 juvs. Reg. no. 1972:556–600. North Europe ? No collection data.
(5) 2♂♂, 4♀♀. Reg. no. 1972:588:6. Murray Firth, Scotland. Leach Collection.
(6) 6♂♂, 1♀, 6 juvs. Reg. no. 1972:559:13. No locality data. No collection data.
(7) 9♂♂, 10♀♀. Reg. no. 1972:567:19. No locality data. No collection data.
(8) 10♂♂, 10♀♀, 20 juvs. Reg. no. 1972:578:40. Baffin Bay, 20.7.1894. University College, Dundee Collection (S.S. *Eclipse*).
(9) Reg. no. 604a, b, d, c, dry collection (Leach cab : 31). Britain. Leach Collection.

Cyamus erraticus Roussel de Vauzème, 1834

(1) 5♂♂, 4♀♀ (immature). Reg. no. 1912:10:2:1–7. 6 miles N.E. of Flugga, Shetland. Collected by Lovett.
(2) 4♂♂, 1♀. Reg. no. 1928:12:1:2966–71. Durban, South Africa, 23.7.1908 ; on *Eubalaena*. T. R. R. Stebbing Collection.
(3) 8♂♂, 10♀♀. Reg. no. 1936:11:2:3532–3541. Saldanha Bay, South Africa, 23.7.1908 ; on *Eubalaena glacialis australis* Desmoulins, whale no. 1020. *Discovery* Collection.

(4) 2♂♂, 5♀♀, 1♀ (immature). Reg. no. 1972:560:8. Rockall, North Atlantic, 1.7.1914; on flipper of *Eubalaena glacialis glacialis* Müller. No collection data.
(5) 14♂♂, 3♀♀. Reg. no. 1972:570:17. No locality data. Albany Museum, Grahamstown Collection.
(6) 1♂. Reg. no. 1972:575:1. No locality data; on *Eubalaena glacialis glacialis* Müller. Collected by Professor Goldberg.

Cyamus gracilis (Roussel de Vauzème, 1834)

(1) 1♂. Reg. no. 1907:12:2:218. Pacific Ocean. University College, Dundee Collection.
(2) 1♀, 1♀ (immature). Reg. no. 1911:11:8:23069–70. No locality data. A. M. Norman Collection.
(3) 8♂♂ (immature), 4♀♀. Reg. no. 1928:12:1:2972–74. False Bay, Cape, South Africa. T. R. R. Stebbing Collection.
(4) 1♂, 6 juvs. Reg. no. 1936:11:2:3582–3584. South Georgia; on *Eubalaena glacialis australis* Desmoulins, whale no. 503. *Discovery* Collection.
(5) Reg. no. 605a (dry collection), Leach cab: 31. British Sea. Leach Collection.

Cyamus monodontis Lütken, 1873

(1) 1 specimen (slide collection). No locality data; on *Monodon monoceros* L. No collection data.
(2) 3♀♀, 10 juvs. Reg. no. 1928:12:1:2975–77. No locality data; on *Monodon monoceros* L. T. R. R. Stebbing Collection.
(3) 2♂♂, 2♀♀. Reg. no. 1911:11:8:23071–74. No locality data; on *Monodon monoceros* L. A. M. Norman Collection.
(4) 5♂♂, 5♀♀, 10 juvs. Reg. no. 1956:10:10:344–346. Davis Straits, Greenland, Canada; on *Monodon monoceros* L. University College, Dundee Collection.
(5) 1♀. Reg. no. 1972:561:1. No locality data. University College, Dundee Collection.
(6) 1♀. Reg. no. 1972:562:1. No locality data; on *Monodon monoceros* L. Collected by Nuttall.
(7) 100♂♂♀♀. Reg. no. 1972:563:100. Upernavik, Greenland, 1892. University College, Dundee Collection.

Cyamus nodosus Lütken, 1860

(1) 4♂♂, 2♀♀ (immature), 14 juvs. Reg. no. 1907:12:2:212–217. Davis Straits, Greenland, Canada. University College, Dundee Collection.
(2) 200♂♂♀♀. Reg. no. 1879:26. Omenak, Greenland; on *Monodon monoceros* L. Collected by E. Whymper.
(3) 2♂♂, 1♀, 1 juv. Reg. no. 1911:11:8:23031–33. Omenak, Greenland. A. M. Norman Collection.
(4) 2♂♂, 4♀♀, 8♀♀ (immature). Reg. no. 1972:564:12. No locality data; on *Monodon monoceros* L. University College, Dundee Collection.

(5) 1♀. Reg. no. 1972:565:1. No locality data; on *Monodon monoceros* L. Collected by Nuttall.
(6) 5♂♂, 3♀♀ (immature), 9 juvs. Reg. no. 1972:566:17. No locality data. University College, Dundee Collection.
(7) 3 specimens (slide collection). No locality data; on *Monodon monoceros* L. No collection data.

Cyamus ovalis Roussel de Vauzème, 1834

(1) 30♂♂♀♀, attached to section of skin. Reg. no. 1911:10:16:1–10. South Georgia, 2.2.1911; on *Eubalaena glacialis* Müller. Collected by G. Cruickshank.
(2) 150♂♂♀♀, attached to section of skin from lower maxilla. Reg. no. 1911:10:16:11–20. South Georgia, 15.3.1911; on *Eubalaena glacialis* Müller. Collected by G. Cruikshank.
(3) 10♂♂, 20 juvs. Reg. no. 1911:11:8:23034–53. Iceland; on *Eubalaena glacialis glacialis* Müller. A. M. Norman Collection.
(4) 2♂♂, 3♀♀, 30 juvs. Reg. no. 1911:11:8:23054–23063. Pacific Ocean; on *Eubalaena glacialis japonica* Lacépède. A. M. Norman Collection.
(5) 150♂♂♀♀, attached to section of skin. Reg. no. 1912:6:15:1–20. South Georgia; on *Eubalaena glacialis australis* Desmoulins. Collected by G. Cruikshank.
(6) 6♂♂, 8♀♀, 30 juvs. Reg. no. 1912:10:2:8–27. 6 miles N.E. of Flugga, Shetland. Collected by Lovett.
(7) 300♂♂♀♀, attached to three separate sections of skin. Reg. no. 1920:10:21:23–42. Stromness Whaling Station, South Georgia; on right whale (upper jaw). Collected by J. Rasmussen and Alex Lange.
(8) 7♂♂, 7♀♀, 6 juvs. Reg. no. 1936:11:2:3483–3494. South Georgia; on *Eubalaena glacialis australis* Desmoulins, whale no. 503. *Discovery* Collection.
(9) 1♂, 2♀♀, 1 juv. Reg. no. 1936:11:2:3483–3494. Saldanha Bay, South Africa, 26.8.1926; on *Eubalaena glacialis australis* Desmoulins, whale no. 1020. *Discovery Collection.*
(10) 10♂♂, 30♀♀, 100 juvs. Reg. no. 1972:571:140. Port Elizabeth. Collected by I. L. Drège.
(11) 3♂♂, 20 juvs. Reg. no. 1972:572:23. Faeröerne Island, North Atlantic, 62° N, 07° W, June 1898; on *Eubalaena glacialis glacialis* Müller, ♀. No collection data.
(12) 2♂♂, 2♀♀. Reg. no. 1972:573:4. No locality data; on *Eubalaena glacialis japonica* Lacépède. Collected by W. N. Lockington.
(13) 7♂♂, 10♀♀, 30 juvs. Reg. no. 1972:574:47. South Georgia; from 'bonnet' of right whale. Collected by P. Stammwitz.
(14) 3♂♂, 9♀♀, 10 juvs. Reg. no. 1972:576:22. No locality data; on *Eubalaena glacialis glacialis* Müller. Collected by Goldberg.
(15) 20 specimens (dry collection). Port Jackson and South Africa. Leach Collection.

Cyamus pacificus Lütken, 1873

(1) 5♂♂. Reg. no. 1877:3. No locality data; on *Megaptera novaeangliae* (Borowski). Collected by W. N. Lockington.

Cyamus scammoni Dall, 1872

(1) 3♂♂, 1♀. Reg. no. 1877:3. No locality data; on *Eschrichtius gibbosus* (Erxleben). Collected by W. N. Lockington.
(2) 30♂♂♀♀, attached to section of skin. Reg. no. 1891:2:10:1–12. Wladiwostock, Victoria Bay, Sea of Japan. Collected by Fridolf Höök.

Cyamus thomsoni Gosse, 1855 see *Platycyamus*

ISOCYAMUS Gervais & Van Beneden, 1859

Isocyamus delphini (Guérin-Méneville, 1836)

(1) 2♂♂. Reg. no. 1911:11:8:23067–68. No locality data; on *Globicephala melaena* Traill (pilot whale). A. M. Norman Collection.
(2) 4♂♂, 5♀♀, 6 juvs. Reg. no. 1936:11:2:3585–3600. 14°45′ N, 18°34′W, 27.10.1925; on *Steno bredanensis* Lesson (rough-toothed dolphin), Dolphin A. *Discovery* Collection.
(3) 1♂, 1♀, 11 juvs. Reg. no. 1936:11:2:3583–3600. 14°45′ N, 18°34′ W, 27.10.1925; on *Steno bredanensis* Lesson, Dolphin B. *Discovery* Collection.
(4) 9♂♂♀♀. Reg. no. 1972:547:9. Tonnybwlch Beach, Aberystwyth, Cardiganshire; on stranded porpoise. Collected by P. Miles.

NEOCYAMUS Margolis, 1955

Neocyamus physeteris (Pouchet, 1888)

(1) 4♀♀. Reg. no. 1965:9:8:46–65. Talcahuano, Chile, 36°45′ S, 73°12′ W, 23.3.1961, on *Physeter catodon* L., ♀ 10·1 m, whale no. T6. Collected by R. Clarke.
(2) 1♂, 2♀♀. Reg. no. 1965:9:8:46–65. Paita, Peru, 05°05′ S, 81°10′ W, 23.6.1959, on *Physeter catodon* L., ♀ 9·6 m, whale no. Pa21. Collected by R. Clarke.
(3) 1♀. Reg. no. 1965:9:8:46–65. Paita, Peru, 05°05′ S, 81°10′ W, 23.4.1960, on *Physeter catodon* L., ♂ 13·7 m, whale no. Pa611. Collected by R. Clarke.
(4) 1♀. Reg. no. 1965:9:8:46–65. Paita, Peru, 05°05′ S, 81°10′ W, 21.4.1959, on *Physeter catodon* L., ♂ 13·3 m, whale no. Pa11. Collected by R. Clarke.
(5) 1♂, 10♀♀, 1 juv. Reg. no. 1965:9:8:46–65. Paita, Peru, 05°05′ S, 81°10′ W, 25.1.1960, on *Physeter catodon* L., ♀ 10·2 m, whale no. 417. Collected by R. Clarke.

PLATYCYAMUS Lütken, 1870

Platycyamus thompsoni (Gosse, 1855)

(1) 1♂. Reg. no. 1907:12:2:219. No locality data. University College, Dundee Collection.

(2) 1♂, 1♀. Reg. no. 1911:11:8:23077–78. No locality data; on *Hyperoodon ampullatus* Forster. A. M. Norman Collection.

(3) 1♂. Reg. no. 1956:10:10:347. No locality data. Collected by University College, Dundee.

(4) Holotype. *Ann. Mag. nat. Hist.* (2) **16** : 30–31. Reg. no. 1856:131 dry coll., Leach cab : 31. Portland Roads S. England; taken from beneath the eye of stranded Bottlenose whale, *Hyperoodon ampullatus* Forster. Leach Collection.

SCUTOCYAMUS Lincoln & Hurley, 1974

Scutocyamus parvus Lincoln & Hurley, 1974

(1) Holotype ♀, 10♀♀ ovig., 21♀♀ immature, 28♂♂, 37 juvs. Reg. no. 1973:105. Off Peterhead, Aberdeenshire, North Sea, 21.7.1933; on *Lagenorhynchus albirostris* Gray (white-beaked dolphin). Collected by Dr F. C. Fraser.

Summary of hosts of whale-lice in the collections

Host	*Whale-lice*
Mysticeti (whalebone whales)	
Gray whale, *Eschrichtius gibbosus* (Erxleben)	*Cyamus scammoni* Dall
Blue whale, *Balaenoptera musculus* (L.)	*Cyamus balaenopterae* Barnard
Fin whale, *Balaenoptera physalis* (L.)	*Cyamus balaenopterae* Barnard
Humpback whale, *Megaptera novaeangliae* (Borowski)	*Cyamus boopis* Lütken *Cyamus pacificus* Lütken
North Pacific right whale, *Eubalaena glacialis japonica* Lacépède	*Cyamus ovalis* R. de Vauzème
Southern right whale, *Eubalaena glacialis australis* Desmoulins	*Cyamus erraticus* R. de Vauzème *Cyamus gracilis* (R. de Vauzème) *Cyamus ovalis* R. de Vauzème
North Atlantic right whale, *Eubalaena glacialis glacialis* Müller	*Cyamus erraticus* R. de Vauzème *Cyamus ovalis* R. de Vauzème
Greenland right whale, *Balaena mysticeti* L.	*Cyamus ceti* (L.)
Odontoceti (toothed whales)	
Sperm whale, *Physeter catodon* L.	*Cyamus boopis* Lütken *Cyamus catodontis* Margolis *Neocyamus physeteris* (Pouchet)
Bottlenose whale, *Hyperoodon ampullatus* Forster	*Platycyamus thompsoni* (Gosse)
Pilot whale, *Globicephala melaena* Traill	*Isocyamus delphini* (Guérin-Méneville)
Narwhal, *Monodon monoceros* L.	*Cyamus monodontis* Lütken *Cyamus nodosus* L.
White-beaked dolphin, *Lagenorhynchus albirostris* Gray	*Scutocyamus parvus* Lincoln & Hurley
Rough-toothed dolphin, *Steno bredanensis* Lesson	*Isocyamus delphini* (Guérin-Méneville)

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A REVIEW OF *LAEPHOTIS* THOMAS, 1901 (CHIROPTERA : VESPERTILIONIDAE)

By J. E. HILL

INTRODUCTION

In recent years the African genus *Laephotis* Thomas, 1901 has been considered monotypic (e.g. Ellerman, Morrison-Scott & Hayman, 1953 : 78) with one subspecies, *L. wintoni wintoni* Thomas, 1901 in Kenya and a second, *L. w. angolensis* Monard, 1935 in Angola, Zambia, Botswana and the southern part of Zaire. However, Peterson (1971) while reporting a further example from Kenya reviewed much of the limited material of *Laephotis* available in collections and was led to suggest that *wintoni* and *angolensis* might represent distinct species, with the possibility that a third undescribed taxon might occur in Zambia. Setzer (1971) treated *wintoni* and *angolensis* as specifically distinct (as had Monard when describing the latter) and described two further species, *namibensis* from the Namib Desert, South West Africa, and *botswanae* from Botswana, Zambia and southern Zaire. Although this author referred to *botswanae* a number of the specimens from Zambia and southern Zaire hitherto allocated to *angolensis*, he did not have available all of the material so reported : in particular he did not examine the specimen (in the Harrison Zoological Museum, Sevenoaks, England) from Ndola, Zambia, which Peterson (1971 : 888) then thought could represent either the then unknown female of *wintoni* or possibly an unnamed taxon. More recently, Peterson (1973 : 602), in describing the first known female of *wintoni* has suggested that the specimen from Ndola may be more closely related to *botswanae* than to other specimens from Zambia or Zaire.

Current accessions to the collections of the British Museum (Natural History) have included three female specimens of *L. wintoni* from Ethiopia, whence the genus has been hitherto unreported. These have led to a further examination of the seven examples of *Laephotis* already in the collections in London, together with six from Zaire in the Musée Royal de l'Afrique Centrale, Tervuren, Belgium, and of two specimens in the Harrison Zoological Museum, one the apparently enigmatic example from Ndola. The four species recognized by Setzer (1971) are retained : *wintoni* and *namibensis* are apparently very similar but differ much more sharply from *angolensis* and *botswanae* than do these from each other.

SYSTEMATIC SECTION

LAEPHOTIS Thomas, 1901

Laephotis Thomas, 1901 : 460.

TYPE SPECIES. *Laephotis wintoni* Thomas, 1901.

Head low, flat-crowned ; muzzle broad, flat, the nostrils opening sublaterally ; ears moderate to large, when laid forward reaching to or beyond the tip of the muzzle, more or less triangular in outline ; anterior margin of the ear originating near the centre of the forehead, lacking any posteriorly directed basal lobe but with a distinct basal fold ; anterior margin convex proximally then less so or nearly straight ; tip rounded ; posterior margin of ear slightly emarginated just below tip, otherwise convex, with moderate rounded or semi-circular antitragal lobe, terminating just behind the angle of the mouth. Tragus (Fig. 1) as a rule rather wide, about one-third the length of the ear, its anterior margin slightly concave, tip bluntly pointed, anteriorly directed ; posterior margin of tragus convex or angular, a small triangular lobe at its base. Calcar extending along about two-thirds of the uropatagial margin, with small, rounded post-calcarial lobe. Seven palate ridges in *L. wintoni* from Ethiopia, the first and second uninterrupted, the last reduced but also complete (Fig. 2) : however, Peterson (1973 : 602, fig. 1) reported six ridges only in a subadult female of *L. wintoni* from Kenya.

Skull with slightly flattened braincase ; slight lambdoid but no sagittal crest ; rostrum rather narrow, unexpanded, with little supraorbital inflation ; a shallow, median rostral depression ; zygomata slender ; narial emargination narrow, broadly U-shaped but slightly angular, extending posteriorly to or a little beyond a line joining the anterior margins of the anteorbital foramina ; pre-palatal emargination extending laterally a little beyond the inner faces of i^{2-2} and posteriorly almost to a line joining the posterior faces of c^{1-1} ; palate long, rather narrow, strongly domed ; maxillary toothrows usually almost parallel ; post-palatal extension moderate to long, its length from a line across the rear faces of m^{3-3} to the tips of the pterygoid hamulars approaching or equal to the length of the palate from the same line to the back of the pre-palatal emargination (Table 2) ; short, broad post-palatal spine ; pterygoid hamulars strong, sharply deflected inwards ; bullae inflated, large.

Dentition $i\,\frac{2}{3}$, $c\,\frac{1}{1}$, $pm\,\frac{1}{2}$, $m\,\frac{3}{3} = 32$. Inner upper incisor (i^2) long, with secondary postero-internal cusp extending almost to its tip ; i^3 small, a little wider than long, its main cusp barely extending above the cingulum of i^2, with small internal basal cusp, in toothrow, touching i^2, separated from c^1 by a narrow space ; c^1 normal ; pm^4 a little wider than long, in contact with c^1 ; m^3 not reduced, with metacone and three commissures ; i_{1-3} tricuspid, imbricated, i_3 slightly the largest ; c_1 reduced, weak, little higher than pm_4 ; pm_2 reduced, about one-half the height and one-quarter or a little more the crown area of pm_4, tightly compressed in toothrow ; m_3 little reduced, the hypoconid and entoconid well developed.

The genus occurs in Ethiopia and Kenya, in southern Zaire, Zambia, Botswana, South West Africa and in Angola. It appears to be related to *Eptesicus*.

Laephotis wintoni Thomas, 1901

Laephotis wintoni Thomas, 1901 : 460. Kitui, Kenya, c. 3500 ft.

Size large for the genus (length of forearm 36–41 mm, condylobasal length 15·2–15·8 mm) with very large ears (length from meatus 21 mm or more) ; tragus broad, at its widest at about one-third of its height from its base, its posterior margin strongly convex, sometimes slightly angular (Fig. 1a). Dorsal surface a shade of mid-brown, the pelage dark based with brown, slightly coppery tips ; ventral surface similar but paler, the hairs similarly dark based but with paler brown or, especially posteriorly, with buffy white tips. Skull elongate with long narrow rostrum ; palate long, the maxillary toothrows nearly parallel ; post-palatal extension very long, its length from a line across the rear faces of m^{3-3} to the tips of the pterygoid hamulars equal or nearly equal to the length of the palate from the same line to the back of the pre-palatal emargination ; bony post-palate long, its length from a line across the rear faces of m^{3-3} to the anterior edge of the mesopterygoid fossa exceeding the distance from the anterior edge of the mesopterygoid fossa to the tips of the pterygoid hamulars (Table 2).

The female of *wintoni* has remained unknown until recently. Peterson (1971 : 888) speculated that a female specimen (1.2533) in the Harrison Zoological Museum, Sevenoaks, from Ndola, Zambia, considerably smaller than the male examples that he had examined, might represent it. Setzer (1971 : 264) noted that data presented by Peterson (p. 886) for specimens of *Laephotis* in the British Museum (Natural History) from Zaire reveal a slight sexual variation, females being on the average a little larger than males in external and cranial measurements. However, the skull had not then been extracted from the sole male specimen (B.M. 57.435, in alcohol) in this series (B.M. 57.435–438) which apparently represents two species (vide infra). The measurements given by Peterson show a female (B.M. 55.1135) from Zambia to be externally a little larger on the whole than a male (B.M. 55.1134) obtained at the same locality but so only in a limited number of cranial dimensions. Peterson (1973 : 601) has reported a subadult female of *wintoni* from Kenya which is comparable to male specimens in most dimensions. The three female specimens of *wintoni* now available from Ethiopia are consistently larger in most respects than two males from Kenya (Table 1) or than the male and subadult female specimens reported from Kenya by Peterson (1971 : 885, 886 ; 1973 : 601). The number of specimens available is too small to establish any firm evidence of sexual variation in size, and the possibility remains that the population of *wintoni* in Ethiopia consists of larger individuals than does the population in Kenya.

The species occurs (Fig. 3) in KENYA (Thomas, 1901 : 460 ; Harrison, 1961 : 292 ; Hayman & Hill, 1971 : 49 ; Peterson, 1971 : 885, 887, fig. 1 (head), pl. 1 (fig. 2) (skull) ; Setzer, 1971 : 262, fig. 1c (tragus)) ; Peterson, 1973 : 601, fig. 1 (soft palate), and in ETHIOPIA (B.M. 72.4397–4399, from Koka, Shoa Province, 8°27′ N, 39°06′ E, at 1700 m).

Laephotis namibensis Setzer, 1971

Laephotis namibensis Setzer, 1971 : 259, 263, fig. 1d (tragus). Kuiseb River, near Namib Desert Research Station, Gobabeb, South West Africa.

No specimens are available for examination, the species being represented at present only by the female holotype and paratype in the collections of the United States National Museum of Natural History at the Smithsonian Institution, Washington. From the description *namibensis* is characterized by its very large ears ; well-developed tragus and antitragus ; pale coloration ; large, relatively long and narrow skull ; relatively long, narrow palate ; and by great inflation of the bullae. It is evidently very similar to *wintoni* but has larger ears (length 24–25 mm) which are broader at the base, and a larger tragus. It is markedly paler in colour than *wintoni*, the dorsal surface pale drab, the ventral surface paler, the hairs tipped with white. Cranially, the braincase is more domed than in *wintoni*, the postorbital region more constricted, the zygomatic arches more arcuate in the vertical plane, the maxillary toothrows more nearly parallel and the bullae more inflated. Although the skull is rather longer than in male specimens of *wintoni* from Kenya, it is only marginally longer than in female specimens from Ethiopia (Table 1).

Laephotis angolensis Monard, 1935

Laephotis angolensis Monard, 1935 : 45. Tyihumbwé (Chiumbwe River, a tributary of the Kasai, 15 km west of Dala), Angola.

Smaller than *wintoni* or *namibensis* (length of forearm 32–35 mm, condylobasal length c. 12·9 mm) with smaller, narrower ears (length from meatus less than 16 mm) ; tragus (Fig. 1b) smaller than in *wintoni* or *namibensis* (vide Setzer, 1971 : 263, fig. 1), less broadened and rather more spatulate. Colour apparently similar to that of *wintoni* but the only available specimens are in alcohol and have been so for some years. According to Setzer (1971 : 260) *namibensis* is paler than *angolensis*. Skull very much smaller than in *wintoni* or *namibensis* (Table 1), the bony part of the post-palatal extension much shorter than in *wintoni*, its length from a line across the rear faces of m^{3-3} to the anterior edge of the mesopterygoid fossa less than the distance from the anterior edge of the mesopterygoid fossa to the tips of the pterygoid hamulars, not exceeding it as in that species (Table 2).

A number of specimens have been allocated hitherto (Hayman & Hill, 1971 : 49) to *angolensis*. These include a further example from Angola, from a locality 35 miles east of Dande, in the collections of the American Museum of Natural History, New York (Hill & Carter, 1941 : 49) which is accepted as representative of *angolensis* by Setzer (1971 : 260 et seq.). Specimens from Zambia, Zaire and Botswana were regarded previously as *angolensis* but Setzer (1971 : 260) took the sole example from Botswana as the holotype of a new species, *botswanae*, to which he referred such of the material from Zambia and Zaire as he was able to examine. Two (B.M. 55.1134–1135) of the three specimens so far reported from Zambia were seen by Setzer : the third is the example (Harrison Zoological Museum 1.2533) discussed by Peterson (1971 : 885, 888 ; 1973 : 602) which apparently also represents *botswanae* (vide infra).

The specimens (B.M. 57.436, 57.438) from Zaire seen by Setzer are from a series of ten collected at Mumene, 70 km east of Lumbumbashi (= Elizabethville), Katanga, which, with a further three from the nearby locality of Musonge, 2 km to the west, were originally reported by Hayman (1957 : 43). This author examined ten of these ; four (B.M. 57.436–438 from Mumene, B.M. 57.435 from Musonge) are in the collections of the British Museum (Natural History) and a further six (M.R.A.C. 26.402–406 from Mumene, M.R.A.C. 26.407 from Musonge) in the Musée Royale de l'Afrique Centrale, Tervuren. Hayman, Misonne & Verheyen (1966 : 50) list nine specimens at Tervuren but no more than six can be found (Thys van den Audenaerde, in litt.), corresponding to the total examined in London by Hayman.

Of these, eight must be referred to *botswanae* but two, B.M. 57.435 and B.M. 57.437 apparently represent not *botswanae* but *angolensis* as it is understood by Setzer (1971 : 260 et seq.). They agree closely with the descriptions of this species by Monard (1935 : 45) and Hill & Carter (1941 : 49) : their measurements (Table 1) are similar to those of the holotype and to those of the second Angolan example as they are reported by Hill & Carter (p. 176) and Setzer (1971 : 261). The specimens differ from the others in the series from Zaire in smaller size, narrower tragus with generally a less angular posterior margin, and in slightly shorter, narrower rostrum and palate. The tragus of B.M. 57.435 is a little wider than that of B.M. 57.437 while among *botswanae* the tragus of M.R.A.C. 26.404 is rather narrow, with its posterior margin a little less angular than is usual in that series. Setzer (1971 : 262) notes that *botswanae* has a more massive rostrum than *angolensis* but the rostrum in B.M. 57.435 and B.M. 57.437 is no more than slightly shorter and not less massive when compared with the narrowest of *botswanae.* The rearward extension of the occipital crests, said by Setzer to be less in *botswanae,* does not differ consistently in the specimens examined. The toothrows of B.M. 57.435 are more divergent posteriorly than those of B.M. 57.437 to approach specimens referred to *botswanae* although, as Setzer notes of this species, its toothrows are generally more divergent posteriorly than in *angolensis.* The specimens available do not confirm the statement by Setzer that the bullae in *botswanae* are relatively as well as actually smaller than in *angolensis* : if B.M. 57.435 and B.M. 57.437 correctly represent *angolensis* then the bullae of *botswanae* are proportionately about the same in size and in actual terms a little larger. That *angolensis* and *botswanae* might occur together was suggested by Setzer (1971 : 262) : records (Fig. 3) of *angolensis* are thus restricted to ANGOLA (Monard, 1935 : 45 ; Hill & Carter, 1941 : 49, 176 ; Setzer, 1971 : 260, 263, fig. 1a (tragus)) and probably ZAIRE (Hayman, 1957 : 43 (in part) ; Hayman, Misonne & Verheyen, 1966 : 50 (in part) ; Peterson, 1971 : 885 (in part)).

Laephotis botswanae Setzer, 1971

Laephotis botswanae Setzer, 1971 : 260, 263, fig. 1b (tragus). 50 miles west, 12 miles south of Shakawe, Botswana.

Size between *angolensis* and the large species *wintoni* and *namibensis* (length of forearm 34–38 mm, condylobasal length (13·5–14·3 mm) ; ears and tragus generally a little larger than in *angolensis* (length of ear from meatus more than 16 but less than 18 mm) but markedly smaller than in either of the large species. Tragus (Fig. 1c) usually with a distinct angularity in its posterior margin at its widest point. Dorsal surface similar in colour to *wintoni* ; ventral surface paler than in that species, the hairs more liberally tipped with buffy white rather than pale brown. Rostrum relatively long, narrow ; maxillary toothrows slightly divergent posteriorly ; postpalatal region as in *angolensis,* the length of its bony part from a line across the rear faces of m^{3-3} to the anterior edge of the mesopterygoid fossa less than the distance from the anterior edge of the mesopterygoid fossa to the tips of the pterygoid hamulars (Table 2).

The specimen (Harrison Zoological Museum 1.2533) from Ndola, Zambia, which Peterson (1971 : 888) thought might represent the female of *wintoni* or possibly an

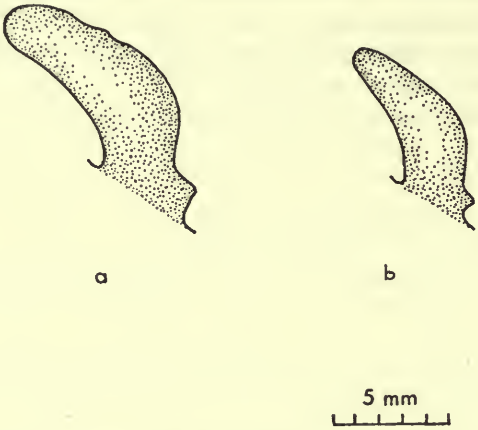

FIG. 1. Tragus of (a) *Laephotis wintoni* ; (b) *L. angolensis* ; (c) *L. botswanae.*

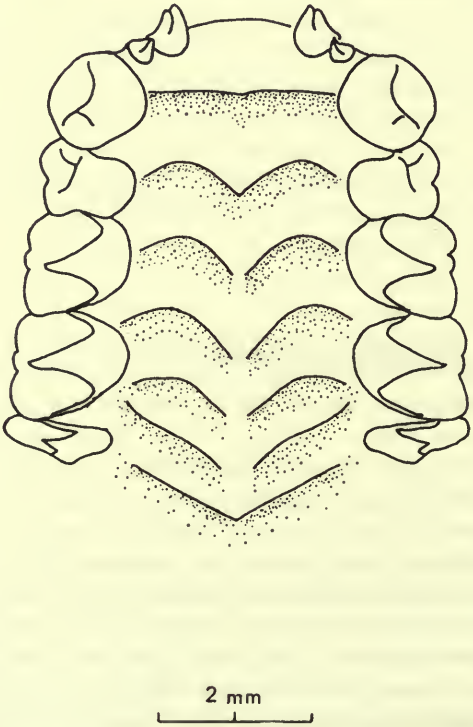

FIG. 2. Palate ridges of *Laephotis wintoni.*

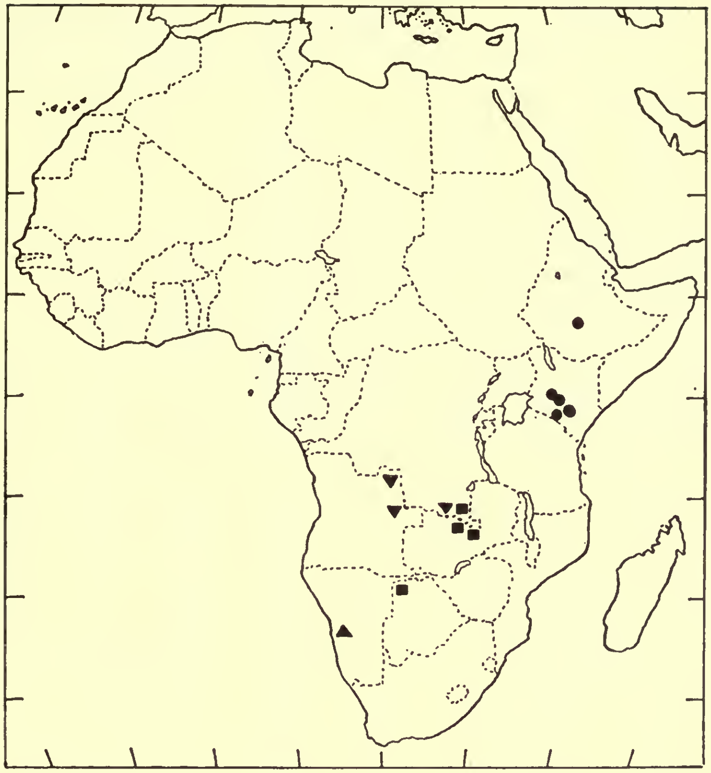

FIG. 3. Distribution of ● *Laephotis wintoni* ; ▲ *L. namibensis* ; ▼ *L. angolensis* ; ■ *L. botswanae.*

undescribed taxon and later (1973 : 602) closely related to *botswanae* proves in fact referable to this species. Although larger than specimens from Zaire or than those (B.M. 55.1134–1135) from Solwezi Boma, Zambia (12°10′S, 26°30′ E) its tragus (from the dry specimen) is angular posteriorly and the specimen agrees precisely in coloration with the other examples from Zambia, differing in this respect from the holotype of *wintoni* in its distinctly paler, more buffy white underparts, especially posteriorly.

Specimens referable to this species have been recorded (Fig. 3) from BOTSWANA (Smithers, 1968 : 48, 49 (map), fig. a (head) (as *angolensis*) ; Setzer, 1971 : 260, 263, fig. 1b (tragus) ; ZAMBIA (Ellerman, Morrison-Scott & Hayman, 1953 : 78 (as *angolensis*) ; Ansell, 1957 : 538 (as *angolensis*) ; Hayman, 1957 : 43 (as *angolensis*) ; Ansell, 1960 : 21 (as *angolensis*) ; Peterson, 1971 : 885, pl. 1 (fig. 2) (skulls, including specimen from Ndola) (as *angolensis* and *Laephotis* sp.) ; Setzer, 1971 : 260) ; ZAIRE (Hayman, 1957 : 43 (in part, as *angolensis*) ; Hayman, Misonne & Verheyen, 1966 : 50 (in part, as *angolensis*) ; Peterson, 1971 : 885 (in part, as *angolensis*) ; Setzer, 1971 : 260).

TABLE I

Measurements (in mm) of *Laephotis*

Registration No.	Sex	Length of forearm	Length of ear from meatus	Greatest length of skull	Condylobasal length	Condylocanine length	Length orbit–gnathion	Width across anteorbital foramina	Width of orbits across lachrimals	Least interorbital width	Zygomatic width	Width of braincase	Depth of braincase	Mastoid width	c^1–c^1	m^3–m^3	c–m^3	Length of complete mandible	c–m_3	Locality
wintoni																				
BM 1.5.6.5*	♂	37·2	–	15·8	15·2	14·9	3·6	4·5	5·2	3·7	–	7·4	4·8	8·5	4·3	5·5	5·0	10·6	5·5	Kenya
HZM 2.3020	♂	36·6	–	15·8	15·2	14·9	3·7	4·6	5·4	3·7	–	7·3	4·8	8·0	4·5	5·7	5·0	10·5	5·4	Kenya
ROM 36368[1]	♂	36·8		16·1	15·4					3·9	9·1		5·0	8·1	4·7	5·9	5·1		5·5	Kenya
ROM 66245[2]	♀	37·8	21	16·0	15·4					3·8	8·4		4·8	8·0	4·3	5·5	4·9		5·4	Kenya
BM 72.4397	♀	40·7	21·4	16·3	15·6	15·4	3·4	4·4	5·5	3·7	8·9	7·4	4·8	8·3	4·5	5·6	5·2	10·8	5·6	Ethiopia
BM 72.4398	♀	40·2	21·1	16·3	15·5	15·4	3·5	4·7	5·4	3·9	9·4	7·5	4·7	8·5	4·6	5·9	5·2	10·7	5·5	Ethiopia
BM 72.4399	♀	40·2	21·5	16·2	15·8	15·6	3·6	4·6	5·3	3·7	9·1	7·6	4·8	8·5	4·5	5·5	5·0	–	5·5	Ethiopia
namibensis																				
USNM 342152*[3]	♀	38·2	25	16·5						3·2	9·0	7·5	4·7		4·0	5·2	4·9			S.W. Africa
USNM 342153[3]	♀	38·6	24	16·5						3·6	–	7·6	4·9		4·0	5·4	5·0			S.W. Africa
angolensis																				
——*[4]		35																		Angola
AMNH 87244[3,5]	♂	32·4	–	13·7						3·4	6·7	6·6	4·4	7·4	4·0	4·9	4·3			Angola
(?) *angolensis*																				
BM 57.435	♂	35·5	16·0	13·8	13·1	12·9	2·8	3·9	4·8	3·4	8·1	6·8	4·5	7·4	3·8	5·2	4·3	8·8	4·8	Zaire
BM 57.437	♀	34·3	15·9	13·7	12·9	12·9	2·8	3·7	4·7	3·5	–	6·8	4·3	7·4	3·7	5·0	4·3	8·9	4·7	Zaire
botswanae																				
USNM 425349*[3]	♀	37·3		14·5						3·4	8·3	7·0	4·7		4·4	5·3	4·7			Botswana
BM 57.436	♀	37·2	17·1	–	–	–	–	4·4	5·0	3·5	–	6·8	–	–	3·9	5·6	4·6	–	5·1	Zaire
BM 57.438	♀	37·6	16·5	–	–	–	3·1	4·3	5·2	3·7	–	–	–	–	4·0	5·7	4·6	–	5·0	Zaire
MRAC 26.402	♀	37·8	16·5	14·5	13·6	13·5	3·1	4·2	5·0	3·7	–	7·4	4·6	7·9	4·0	5·4	4·5	9·4	4·9	Zaire
MRAC 26.403	♀	35·8	16·3	14·3	13·5	13·4	3·0	4·2	5·1	3·7	–	7·3	4·6	7·6	4·0	5·4	4·6	9·1	4·9	Zaire
MRAC 26.404	♀	37·0	16·8	14·6	13·7	13·6	3·1	4·1	5·1	3·5	–	7·1	4·6	7·8	4·0	5·4	4·5	9·5	5·0	Zaire
MRAC 26.405	♀	36·4	17·9	14·3	13·6	13·5	3·0	4·1	4·9	3·6	–	7·2	4·7	7·8	3·8	5·2	4·5	9·2	5·0	Zaire
MRAC 26.406	♀	36·1	17·1																	Zaire
MRAC 26.407	♀	36·7	17·4																	Zaire
BM 55.1134	♂	34·2	–	–	13·8	–	3·0	4·1	5·0	3·7	–	7·0	4·5	7·3	–	–	–	–	5·1	Zambia
BM 55.1135	♀	35·3	–	14·3	13·5	13·4	3·1	4·2	5·3	3·6	–	7·1	4·5	7·5	4·0	5·5	4·6	9·2	4·9	Zambia
HZM 1.2533	♀	37·0	–	15·0	14·3	14·2	3·1	4·5	5·5	3·7	8·8	7·4	4·6	8·4	4·3	5·8	4·8	9·9	5·2	Zambia

BM	British Museum (Natural History), London.
HZM	Harrison Zoological Museum, Sevenoaks.
ROM	Royal Ontario Museum, Toronto.
USNM	United States National Museum of Natural History, Washington.
AMNH	American Museum of Natural History, New York.
MRAC	Musée Royale de l'Afrique Centrale, Tervuren.

* Holotype.

[1] Peterson, 1971 : 886.

[2] Peterson, 1973 : 601.

[3] Setzer, 1971 : 261.

[4] Monard, 1935 : 47.

[5] Hill & Carter, [illegible]

TABLE 2

Palatal measurements (in mm) of *Laephotis*

Registration No.	Sex	Palatal length	Length from rear of pre-palatal emargination to anterior edge of mesopterygoid fossa	Length from rear of pre-palatal emargination to line across posterior faces of m^{3-3}	Length from line across posterior faces of m^{3-3} to anterior edge of mesopterygoid fossa	Length from anterior edge of mesopterygoid fossa to tip of pterygoid hamulars	Length from line across posterior faces of m^{3-3} to tip of pterygoid hamulars	Locality
wintoni								
BM 1.5.6.5*	♂	7·9	6·5	4·4	2·1	1·9	4·0	Kenya
HZM 2.2030	♂	–	–	–	–	–	–	Kenya
BM 72.4397	♀	8·1	6·8	4·4	2·4	1·8	4·2	Ethiopia
BM 72.4398	♀	8·2	6·4	4·2	2·2	2·0	4·2	Ethiopia
BM 72.4399	♀	8·5	6·8	4·3	2·5	1·9	4·4	Ethiopia
(?) *angolensis*								
BM 57.435	♂	6·2	4·8	3·6	1·2	2·0	3·2	Zaire
BM 57.437	♀	6·1	4·8	3·5	1·3	1·9	3·2	Zaire
botswanae								
BM 57.436	♀	–	5·4	4·0	1·4	–	–	Zaire
BM 57.438	♀	6·7	5·2	3·8	1·4	2·0	3·4	Zaire
MRAC 26.402	♀	6·6	5·2	3·7	1·5	2·0	3·5	Zaire
MRAC 26.403	♀	6·6	5·2	3·7	1·5	1·9	3·4	Zaire
MRAC 26.404	♀	6·4	5·2	3·8	1·4	1·9	3·3	Zaire
MRAC 26.405	♀	6·5	5·3	3·8	1·5	1·9	3·4	Zaire
BM 55.1134	♂	6·5	5·2	3·7	1·5	–	–	Zambia
BM 55.1135	♀	6·4	5·2	3·7	1·5	1·9	3·4	Zambia
HZM 1.2533	♀	7·1	5·6	4·1	1·5	2·0	3·5	Zambia

BM	British Museum (Natural History), London.
HZM	Harrison Zoological Museum, Sevenoaks.
MRAC	Musée Royale de l'Afrique Central, Tervuren.

* Holotype.

SUMMARY

The majority of specimens of *Laephotis* hitherto reported in the literature are allocated to the appropriate one of the four species recognized in the most recent study of this genus, and these are briefly reviewed. Female specimens of *L. wintoni* are recorded from Ethiopia, whence until now the genus has been unreported.

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THE GENUS *FINMARCHINELLA* SWAIN 1963 (CRUSTACEA: OSTRACODA) AND ITS SPECIES

By JOHN W. NEALE

SYNOPSIS

Six species of the genus *Finmarchinella* from the Northern Hemisphere are found to fall into two groups for one of which the new subgenus *Barentsovia* is instituted. The confusion surrounding the four North Atlantic and Arctic species is analysed and the new species *Finmarchinella* (*Barentsovia*) *curvicosta* is described.

INTRODUCTION

In 1963 Swain established the genus *Finmarchinella* with *Cythereis finmarchica* Sars 1866 as the type species. In 1957, however, Mandelstam had described the new species *Nereina barentzovoensis* from Russian Harbour, Novaya Zemlya, as the genotype of his new genus *Nereina*. In 1966 Ishizaki pointed out that *Nereina* was used for a gastropod described by Cristofori and Jan in 1832 and that Mandelstam's genus required a new name. The following year, Hazel (1967a, p. 18) examined the classification of Recent Hemicytheridae from off North-eastern North America and regarded *Finmarchinella finmarchica* and *Nereina barentzovoensis* as congeneric placing them both in *Nereina* and considering *Finmarchinella* to be a junior synonym. Subsequently Hazel (1967b) noted that *Nereina* was preoccupied and since *Finmarchinella* was available he validated Swain's genus which thus contained these two species and *Cythereis angulata* Sars 1866. In addition *Nereina japonica* Ishizaki 1966 from the Miocene and Pliocene of Japan and *Finmarchinella uraniponnica* Ishizaki 1969 from the Recent seas of western Honshu also belong here. These five species, together with a new Arctic species fall into two distinct groups. *F. finmarchica* and *F. uraniponnica* are regarded as falling within the strict interpretation of *Finmarchinella*; the remaining four species are separated and placed in the new subgenus *Barentsovia* based on *F.* (*B.*) *barentzovoensis* (Mandelstam).

The principal aim of this paper, however, is to sort out the confusion that has arisen between the occidental species of the subgenus *Barentsovia* and place their taxonomy on a sound footing. This has been done on the basis of carapace characters since soft parts have not been available for study in most species. The uncontroversial *Finmarchinella* s.s. group is dealt with first.

LOCATION OF MATERIAL

Specimens preceded by 'BM' are in the collections of the British Museum (Natural History), those preceded by 'HU' are in the collections of Hull University.

SYSTEMATIC DESCRIPTIONS

Genus *FINMARCHINELLA* Swain 1963

TYPE SPECIES. *Cythereis finmarchica* Sars 1866.

Subgenus *FINMARCHINELLA* Swain 1963

Finmarchinella (F.) finmarchica (Sars 1866)

(Pl. 1, figs. 6, 7 ; Pl. 2. figs. 1, 5 & 11)

Cythereis finmarchica Sars, 1866 : 41.
Hemicythere finmarchica, G. O. Sars, Sars, 1925 : 185–6, pl. LXXXV, fig. 3.

DIMENSIONS OF FIGURED SPECIMENS.

	Catalogue no.	Figure	Length (mm)	Height (mm)	Width (mm)
Male left valve	B.M. No. M 3287A	Pl. 1, fig. 6	0·688	0·331	–
Female left valve	B.M. No. M 3287B	Pl. 1, fig. 7 Pl. 2, fig. 11	0·720	0·392	–
Male carapace	B.M. No. M 3287C	Pl. 2, fig. 1	0·701	0·328	0·318
Female carapace	B.M. No. M 3287D	Pl. 2, fig. 5	0·746	0·405	0·389

DISCUSSION. This species presents no difficulties in interpretation and only the original reference and the original author's later figure are given here in the synonymy. The characteristic features are the rather 'smoothed-out' appearance with well-developed reticulation and pitting but a lack of strong costation. In dorsal view the outline is smooth and more oval than in species of the subgenus *Barentsovia* (cf. Pl. 2, figs. 1, 5 and Pl. 2, figs. 2–4). As in other species of the genus, sexual dimorphism is very marked with the males much slimmer and lower in proportion to the length than the females (Pl. 1, figs. 6, 7 ; Pl. 2, figs. 1, 5).

DISTRIBUTION. Since this species has not hitherto been confused with any other it is possible to use records in the literature to plot its distribution with some confidence (Fig. 1). Sars originally described *F. finmarchica* from some empty shells from shell sand in Oxfjord, Finmark, and subsequently found it at Korshavn on the Norwegian coast further south. Besides Sars localities it has been found in Vadsö and Lang Fjords (Brady & Norman, 1896, appendix). In the Norwegian and Barents Sea areas the author has found it in samples from Ernest Holt Station 2 (70°29′ N, 17°27′ E) where it accounted for 2·18 per cent of the specimens, Station 6 (69°54′ N, 17°00′ E, 1·62 per cent of the fauna), H.M.S. *Vidal* Station 29 (c. 68°44′ N, 41°23·5′ E) and Station 46 on the Spitzbergen Shelf (75°11·2′ N, 22°14′ E, 16·47 per cent). Widely distributed in high latitudes, it was recorded from three localities in the Davis Strait and has been found in material from the Hunde Islands (68°52′ N, 53°07′ W, 1·58 per cent), Holsteinsborg Harbour, Greenland (66°55′ N, 53°25′ W, 7·73 per cent), off Cape Flora, Franz Joseph Land (79°57′ N, 50°01′ E, 1·25 per cent) and Russian Harbour, Novaya Zemlya (76°13′ N, 62°40′ E, 0·97 per cent). Hazel (1967a) found it at Ungava Bay (60°08′ N, 67°47′ W) and gives a number of localities in the Gulf of Maine and on the Atlantic Shelf (Hazel, 1967a, 1970). It was fairly widely recorded round Scotland and England by Brady (1868) and Brady and Norman (1889), many of whose records can be confirmed by reference to material in the Hancock Museum, Newcastle-upon-Tyne ; Ostenfeld and Wesenberg-Lund (1909)

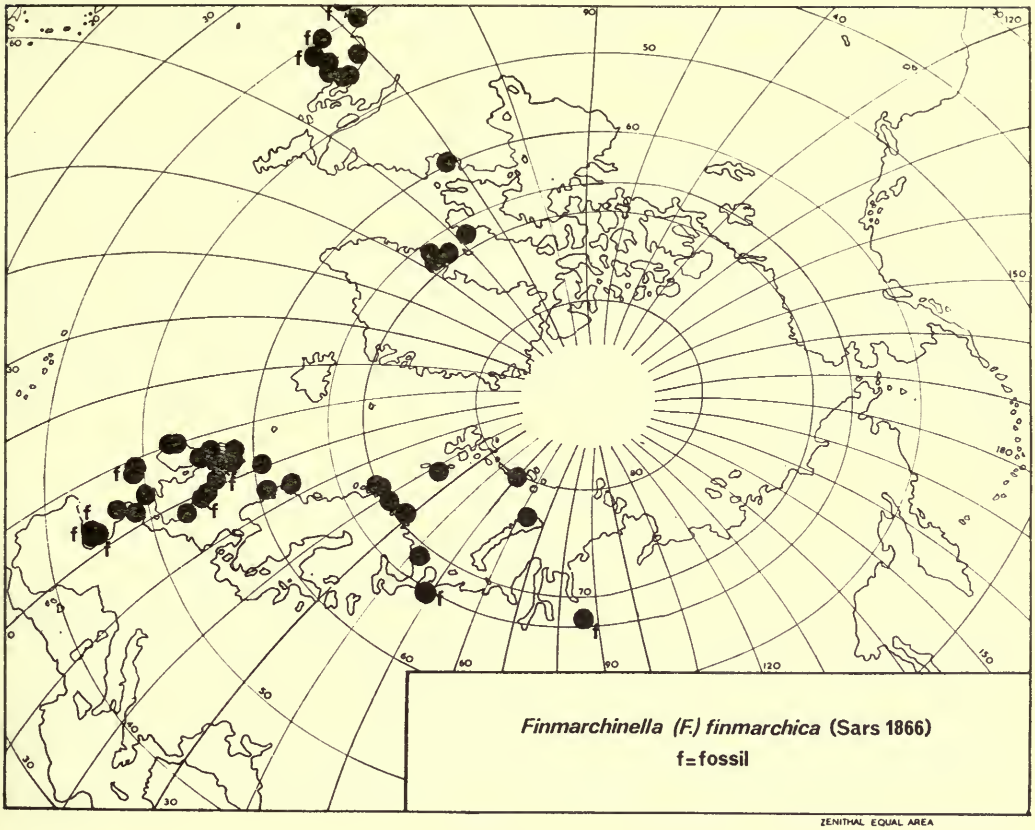

Fig. 1

note it from the North Sea and the author has found it in the Celtic Sea in core sample 5652 (49°38′ N, 9°19′ W) and from both top and bottom of the 88 cm core sample 5674 (49°50·9′ N, 9°08′ W). Vos (1957) added the Château du Taureau (entrance to the River Morlaix Estuary). It has been widely encountered in the Bay of Biscay (Peypouquet, 1971b, gives 22 localities) but it is always rare and Peypouquet (1971a) and Moyes & Peypouquet (1971) regard it as representing a palaeothanatocoenose of Holocene and Pleistocene age. This could explain the record from St Vincent, Cape Verd, by Brady & Norman (1889) but on balance one is inclined to agree with Hazel (1967a) who thought that it was most probably a mis-identification. It is well known as a fossil in the post-Tertiary deposits of Britain (Brady, Crosskey & Robertson, 1874), Hazel (1968) has found it in the Pleistocene of a number of submarine canyons off the eastern seaboard of the United States and Lev (1969) has found it in his *Normanicythere concinella* community in the Kazantsevian deposits of the right bank of the River Yenesei and Cheshkaya Bay. Thus, *F. finmarchica* is essentially an Arctic and boreal-Arctic species whose southern limit appears to be about Ushant (Vos figures soft parts from the Château du Taureau locality).

Finmarchinella (Finmarchinella) uraniponnica Ishizaki 1969

Finmarchinella uraniponnica Ishizaki, 1969 : 217–218, pl. 26, figs. 12, 13 ; pl. 24, fig. 4 ; Ishizaki, 1971 : 83, pl. 3, fig. 3.

This species is most easily differentiated from *F. finmarchica* by its more asymmetrical anterior and more sloping posterior margins in lateral view. The slight concavity in the anterior half of the ventral margin seems a little more accentuated also.

Not so far recorded outside Honshu, it appears to be rather rare in Western Honshu where it was only found at one station in the Nakanoumi Estuary. Here it was accompanied by *Cushmanidea subjaponica* and *Hermanites tosaensis* which were also confined to this station, and seventeen other species which had a much wider distribution. In N.E. Honshu in Aomori Bay, however, Ishizaki (1971) has shown that it occurs much more commonly.

Subgenus ***BARENTSOVIA*** subgen. nov.

TYPE SPECIES. *Finmarchinella barentzovoensis* (Mandelstam, 1957).

DIAGNOSIS. A subgenus of *Finmarchinella* which differs from *Finmarchinella* s.s. in the development of marked costation, particularly in the posterodorsal part of the valve and in the prominent development of the subcentral and eye tubercles.

As shown below, the three occidental species of *Barentsovia* have been the subject of confusion amongst themselves and it is impossible to use the records in the literature to establish their distribution unless there are accompanying illustrations which show the distinctive features. In consequence the distributions on the map (Fig. 2) use only the latter and material actually verified by the author.

Finmarchinella (Barentsovia) barentzovoensis (Mandelstam, 1957)

(Pl. 1, figs. 4, 5, 9 ; Pl. 2, fig. 12)

Cythere clathrata, Reuss var. *nuda* Brady, 1866 : 376–377, pl. 59, figs. 9, 10.
Hemicythere angulata (Sars) Akatova, 1946 : 227, fig. 5.
Nereina angulata (Sars) Hazel, 1967 (pars) : 19, pl. 1, figs. 7, 11. (non pl. 1, figs. 8, 9, 10 = *F.* (*B.*) *curvicosta*.)
Nereina barentzovoensis Mandelstam, 1957 : 180, pl. 3, figs. 7, 8.

DIMENSIONS OF FIGURED SPECIMENS.

	Catalogue no.	Figure	Length (mm)	Height (mm)
Male left valve	HU. 80.R.23	Pl. 1, fig. 4	0·766	0·392
Female left valve	HU. 80.R.24	Pl. 1, fig. 5	0·831	0·457
Female left valve	HU. 80.R.25	Pl. 1, fig. 9 Pl. 2, fig. 12	0·821	0·447

DISCUSSION. This species has been confused with *F.* (*B.*) *angulata* (Sars). The earliest record of this species is that of Brady (1866) who figured it as a variety of

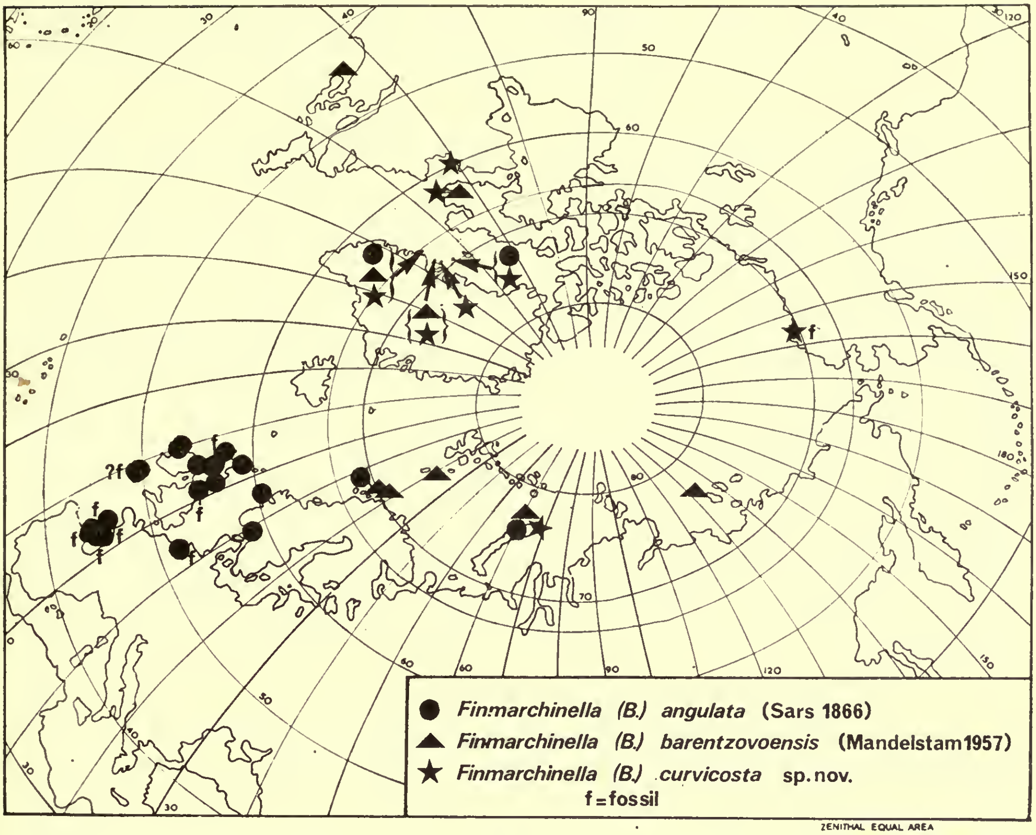
● Finmarchinella (B.) angulata (Sars 1866)
▲ Finmarchinella (B.) barentzovoensis (Mandelstam 1957)
★ Finmarchinella (B.) curvicosta sp. nov.
f = fossil
?f
ZENITHAL EQUAL AREA

FIG. 2

Cythere clathrata Reuss which he called *nuda*, giving as localities the Hunde Islands and Norway. His figures show the characteristic ornamentation and this is confirmed by a slide from the Hunde Islands in the Brady Collection in the Hancock Museum labelled '*Cythere angulata* ? Sars = var : *nuda* Brady'. This contains five specimens, male and female right valves and two female left valves of *F.* (*B.*) *barentzovoensis* and a female right valve of *F.* (*B.*) *angulata* (Sars). Later Brady & Norman (1889) placed *Cythere clathrata* var. *nuda* in synonymy with Sars' species and the confusion has persisted. Akatova (1946) figured a specimen as *Hemicythere angulata* (G. O. Sars). More recently Hazel (1967a), commenting on the difficulty of interpreting Mandelstam's species from the published figures and lacking comparative material, figured two specimens of this species as *Nereina angulata* (Sars). The differences, however, are clear and well seen by comparing Pl. 1, figs. 4, 5 with Pl. 2, fig. 8, and Pl. 2, figs. 10, 12. The species is most easily recognized in lateral view by the strong rib which follows the anterior margin in its dorsal half and then curves in to the body of the valve at about mid-height. The posterodorsal quarter of the valve surface is also particularly distinctive with two oblique ribs which run posterodorsally from the subcentral tubercle and are linked by a very well-developed inflation or tubercle at their posterodorsal termination. The lower of these two ribs is the stronger.

DISTRIBUTION. Mandelstam's original material came from Russian Harbour, Novaya Zemlya, and material from this locality collected by Professor H. V. Howe in 1937 yielded 146 excellent specimens (46 per cent of them adults) of which three are figured here. Hazel's specimens came from Frobisher Bay (63°10′ N, 67°45′ W) and the Gulf of Maine (44°08′ N, 68°13′ W). Akatova figured a specimen from station 80 on the Novosiberian Shelf (76°52′ N, 133°23′ E). The present author has found it in British Museum (N.H.) samples collected by the 'Ernest Holt' at Stations 1 (70°32′ N, 18°23′ E) and 6 (69°54′ N, 17°00′ E) and by H.M.S. *Vidal* at Station 46 (75°11·2′ N, 22°14′ E) on the Spitzbergen Shelf, and in material from the Hunde Islands (68°52′ N, 53°07′ W) in the Hancock Museum. The distribution of *F.* (*B.*) *barentzovoensis* is essentially Arctic (Fig. 2), all the records (except for the somewhat anomalous specimen from the Gulf of Maine figured by Hazel) being from latitudes higher than 63° N and the maximum depth at which it has been recorded is 143 fathoms (Ernest Holt Station 6), the bulk of the occurrences being between 10–40 fathoms. It may thus be regarded as a relatively shallow-water Arctic form and it is possible that Hazel's Gulf of Maine right valve is a sub-Recent specimen.

Finmarchinella (Barentsovia) angulata (Sars 1866)

(Pl. 1, fig. 8 ; Pl. 2, figs. 2, 4, 6 & 10)

Cythereis angulata G. O. Sars, 1866 : 46.

Cythere angulata (Sars), Brady, 1868 : 409, pl. 26, figs. 39–42 ; Brady, Crosskey & Robertson, 1874 : 162–163, pl. 4, figs. 17–24, pl. 10, fig. 22 ; Brady & Norman, 1889 (pars) : 165 (non *Cythere clathrata*, var. *nuda*, Brady = *F.* (*B.*) *barentzovoensis*).

Hemicythere angulata, G. O. Sars, Sars, 1925 : 187–188, pl. LXXXVI, fig. 2.

'*Hemicytherinae*' (genre ?) *angulata* (Sars), Wagner, 1957 : 61–62, pl. XXXVIII, figs. 1, 2 ; Yassini, 1969 : 42–43, pl. XXXIX, fig. 17.

Non *Hemicythere angulata* (G. O. Sars), Akatova, 1946 : 227, fig. 5 (= *F.* (*B.*) *barentzovoensis*).

Non *Finmarchinella angulata* (Sars), Swain, 1963 : 813 (pl. 97, fig. 22 = juv. indet. ; pl. 99, fig. 9 & text-fig. 11c. = *F.* (*B.*) *curvicosta*).

Non *Nereina angulata* (Sars, 1865), Hazel, 1967 : 19 (pl. 1, figs. 7, 11 = *F.* (*B.*) *barentzovoensis* ; pl. 1, figs. 8, 9, 10 = *F.* (*B.*) *curvicosta*).

DIMENSIONS OF FIGURED SPECIMENS.

	Catalogue no.	Figure	Length (mm)	Height (mm)	Width (mm)
Female left valve	Oslo Museum F 1447.4	Pl. 1, fig. 8 Pl. 2, fig. 10	0·704	0·380	–
Female right valve	Oslo Museum F 1447.6	Pl. 2, fig. 6	0·668	0·357	–
Male carapace	B.M. No. 1973.331	Pl. 2, fig. 2	0·701	0·367	0·325
Female carapace	B.M. No. 1973.332	Pl. 2, fig. 4	0·740	0·415	0·377

DISCUSSION. This species has been confused with both *F.* (*B.*) *barentzovoensis* and *F.* (*B.*) *curvicosta* in the past. Sars' illustration in the *Crustacea of Norway* (1925, pl. LXXXVI, fig. 2) shows a rib which slightly affects the lateral outline posterodorsally. Sars (1925, p. 188) notes that he had taken this species 'in several places on the Norwegian coast from Christiana Fjord to Finmark, in the laminaria zone, though nowhere in any abundance'. The type material could not be traced but the Zoologisk Museum, Oslo, kindly searched its collections and provided a phial of spirit material labelled in Sars' own hand '*Hemicythere angulata* G.O.S.' This yielded 13 specimens of *F.* (*B.*) *angulata* including four juveniles which showed that Sars' figure emphasized the essential features. Dorsally there is a rib which runs from approximately the mid-length of the valve towards the posterodorsal cardinal angle where it becomes accentuated, often affecting the outline posterodorsally in lateral view. The rib then turns downward at almost a right angle, or even more acutely, before disappearing at about mid-height (Pl. 1, fig. 8a ; Pl. 2, fig. 10). The posterior part of the dorsal margin is slightly concave in lateral view.

F. (*B.*) *angulata* is most easily differentiated from *F.* (*B.*) *barentzovoensis* and *F.* (*B.*) *curvicosta* by the lack of any rib connecting the ventral end of this posterodorsal accentuation with the subcentral tubercle. Sars' material also shows the presence of a marginal rib anteriorly (Pl. 1, fig. 8a) which coincides with the outline at the anterior cardinal angle and ventrally, but lies some distance inside anteriorly where it follows the general curve of the outline but with the dorsal two-thirds forming a much flatter arc. This species also lacks the incurved part of the anterior rib at about mid-height which is characteristic of *F.* (*B.*) *barentzovoensis*.

DISTRIBUTION. Sars found this species living in shallow water along the length of the Norwegian coast. It occurs at Russian Harbour, Novaya Zemlya, and Ernest Holt Station 6 in the Barents and Norwegian Sea areas and the author has also found juveniles in Cockburn Bank samples 5668 (49°50′ N, 9°18′ W) and 5673 (49°50′ N, 9°09′ W) although these Celtic Sea specimens are possibly not indigenous. Slides in the British Museum (N.H.) show that in the Greenland area it was found at Holsteinsborg Harbour (where it occurred with almost equal numbers of *F.* (*B.*) *curvicosta*) and at Station 3 (69°31′ N, 56° 01′ W) of H.M.S. *Valorous* in 1875 ; in the Norwegian area at Hollingpollen, Dröbak and Lungegaards-vandet, Bergen ; and round the Irish and Scottish coasts at Clew Bay, County Mayo, between the Cumbraes in the Firth of Clyde, off Tarbert, Loch Fyne and in the Minch. From the Brady Collection in the Hancock Museum, Newcastle-upon-Tyne, it has been possible to verify the presence of this species in the Hunde Islands in the Greenland region ; in Stromness Bay, Scapa Flow, Rothesay Bay, Cumbrae, Rosneath, and Bo'ness in the Firth of Forth in the Scottish area and in Westport Bay in Ireland. From the same collection one can also confirm that it occurs fossil at Loch Gilp, Dalmuir, Colintraive, Cumbrae and in raised beaches at Oban and Tarbert. It also occurs fossil in the Quaternary of the Netherlands (Wagner, 1957) and Yassini (1969) found it at eight localities in the Bay of Biscay although he did not regard it as living in that area at the present day. Most records of this species are from less than 50 fathoms and only rarely has it been found at depths of more than 100 fathoms. Its known occurrence is shown in Fig. 2.

Finmarchinella (Barentsovia) curvicosta sp. nov.

(Pl. 1, figs. 1–3 ; Pl. 2, figs. 3, 7–9, 13)

Finmarchinella angulata (Sars) Swain, 1963 : 813–814, pl. 99, fig. 9 & text-fig. 11c. non pl. 97, fig. 22 (= juv. indet.)

Nereina angulata (Sars) Hazel, 1967 (pars) : 19, pl. 1, figs. 8, 9, 10. non pl. 1, figs. 7, 11 (= *F.* (*B.*) *barentzovoensis*).

HOLOTYPE. A female carapace (mounted as separate valves) from Holsteinsborg Harbour, Greenland, B.M. No. 1973.310.

PARATYPES. Nineteen specimens from Holsteinsborg Harbour, Greenland, including males, females and juveniles, B.M. Nos. 1973.311–329.

OTHER MATERIAL. Fifty-two specimens in the collections of Hull University and Louisiana State University.

DIMENSIONS OF FIGURED MATERIAL.

	Catalogue no.	Figure	Length (mm)	Height (mm)	Width (mm)
Female left valve, holotype	B.M. No. 1973.310	Pl. 1, fig. 3 Pl. 2, fig. 13	0·808	0·451	–
Male left valve, paratype	B.M. No. 1973.311	Pl. 1, fig. 2	0·743	0·383	–
Female right valve, paratype	B.M. No. 1973.312	Pl. 1, fig. 1 Pl. 2, fig. 8	0·844	0·450	–
Female left valve, paratype	B.M. No. 1973.313	Pl. 2, fig. 9	0·844	0·454	–
Female carapace, paratype	B.M. No. 1973.314	Pl. 2, fig. 3	0·811	0·441	0·431
Female left valve	HU. 80.R.26	Pl. 2, fig. 7	0·876	0·506	–

DIAGNOSIS. A species of *Finmarchinella* (*Barentsovia*) with gently convex posterodorsal margin, well-developed costation and overall reticulation. An almost horizontal rib runs posteriorly from the subcentral tubercle to about five-sixths of the length where it joins a strong curved rib at an acute angle. The curved rib passes into a weaker oblique rib which runs back to the subcentral tubercle. The elongate loop formed by these costae usually contains two rows of polygonal fossae. Dorsal and ventral ribs complete the principal costation.

DESCRIPTION. Valves in lateral view rounded-rectangular of typical *Finmarchinella* shape. Posterodorsal margin gently convex, posterior margin concave. In dorsal view rounded subhexagonal. Eye tubercles and subcentral tubercle well-developed. Ornamentation of overall reticulation consisting of finely pitted polygonal fossae and costation. There are four principal costae, the most prominent of which is an almost horizontal rib which runs posteriorly from the subcentral tubercle. At about five-sixths the length this joins at an acute angle a short, curved, accentuated rib which runs towards the middle of the dorsal margin and generally forms the most prominent feature of the ornamentation. Dorsally, this strong, curved rib runs into a relatively weak oblique rib which runs anteroventrally back to the subcentral tubercle. This straight section of the curved rib is the most weakly developed of the principal costae. As a whole the costate pattern in this area forms an elongated loop with its apex at the subcentral tubercle. The loop normally contains two rows of polygonal fossae. A third principal rib starts just below the posterior part of the eye tubercle and runs obliquely in a posterodorsal direction to join the dorsal margin at about three-quarters of the length (Pl. 1, fig. 2a; Pl. 2, fig. 3). A fourth, slightly flexuous costa delimits the junction between the lateral and ventral surfaces and is very prominent at its posterior termination. Hinge antimerodont, anterior and posterior toothplates with 5–6 (usually 5) teeth and median locellate groove in the right valve. Left valve with complementary structures. Normal pore canals large, simple and scattered. Marginal pore canals simple and straight; approximately 36 anteriorly and 10 posteriorly. Anterior and posteroventral vestibules exceedingly narrow. Muscle scar pattern typical of the genus consisting of a vertical row of four adductor scars with three scars anteriorly. The long axes of the adductor scars lie obliquely to the length of the valve, declining anteriorly. The middle scars are very clearly divided. Sexual dimorphism marked, the males being lower in proportion to their length than the females.

AFFINITIES AND DIFFERENCES. This species is most closely related to the two preceding species. It is most easily differentiated by the posterodorsal margin which is convex in lateral view compared with the concavity in this region seen in *F.* (*B.*) *barentzovoensis* (Pl. 1, figs. 4, 5) and *F.* (*B.*) *angulata* (Pl. 1, fig. 8a). Besides other differences in ornamentation *F.* (*B.*) *curvicosta* lacks the prominent incurving of the anterior rib of *F.* (*B.*) *barentzovoensis* and the curve of the posterodorsal rib is much flatter and lies well below the valve margin compared with *F.* (*B.*) *angulata* (cf. Pl. 2, figs. 13 and 10).

DISTRIBUTION. *F.* (*B.*) *curvicosta* is essentially Arctic in distribution (Fig. 2). Slides in the British Museum (N.H.) show that it occurs in 10 fathoms at Holsteinsborg Harbour and 5–25 fathoms at Godhavn Harbour, Disco in the Greenland area and was dredged from 100 fathoms at Station 3 (69°31′ N, 56°01′ W) by H.M.S. *Valorous* in 1875. The Brady Collection in the Hancock Museum, Newcastle-upon-Tyne, contains a slide of this species from the Hunde Islands (68°52′N, 53°07′ W), also in the Greenland area. It occurs at Kneeland Bay (62°59′ N, 67°28′ W) and Ungava Bay (60°08′ N, 67°47′ W) where it was recorded by Hazel (1967a) as *Nereina angulata* (Sars) and Swain (1963) figured a female left valve from the Pleistocene Gubik Formation of Alaska, also as *Finmarchinella angulata* (Sars). In the eastern hemisphere it was found quite commonly in 8 fathoms at Russian Harbour, Novaya Zemlya.

Finmarchinella (Barentsovia) japonica (Ishizaki, 1966)

Nereina japonica Ishizaki, 1966: 143–144, pl. 19, figs. 1–4, text-fig. 1, figs. 3, 4.

DISCUSSION. This species shows the well-developed submedian and eye tubercles of *Barentsovia*. The costation is difficult to ascertain from the figure of the holotype but in his description Ishizaki notes that the dorsal rib extends to the posterior end where it turns downward and disappears at mid-height. This, coupled with the general reticulation, is much more reminiscent of *F.* (*B.*) *angulata* (Sars) than of the other species of *Barentsovia*. It differs from *F. angulata* in the more prominent ventral rib.

Ishizaki's species is exclusively fossil and has not so far been found outside the Miocene and Pliocene of Japan.

CONCLUSIONS

The genus *Finmarchinella* is essentially a cold water genus which includes non-costate (s.g. *Finmarchinella*) and costate (s.g. *Barentsovia*) groups. The confusion between species of the latter is easily resolved by reference to the shape and ornamentation of the valves.

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PLATE 1

Finmarchinella

Magnification in all cases × 72 ± 4

FIG. 1. *Finmarchinella* (*B.*) *curvicosta* sp. nov. Paratype. Female right valve, B.M. No. 1973.312. a. Internal lateral view, b. Oblique dorsal internal view. Holsteinsborg Harbour, Greenland.

FIG. 2. *Finmarchinella* (*B.*) *curvicosta* sp. nov. Paratype. Male left valve, B.M. No. 1973.311. a. External lateral view. b. Oblique anterior view. Holsteinsborg Harbour, Greenland.

FIG. 3. *Finmarchinella* (*B.*) *curvicosta* sp. nov. Holotype. Female left valve of carapace, B.M. No. 1973.310. a. External lateral view. b. Oblique anterior view. Holsteinsborg Harbour, Greenland.

FIG. 4. *Finmarchinella* (*B.*) *barentzovoensis* (Mandelstam). Male left valve, HU. 80.R.23. External lateral view. Russian Harbour, Novaya Zemlya.

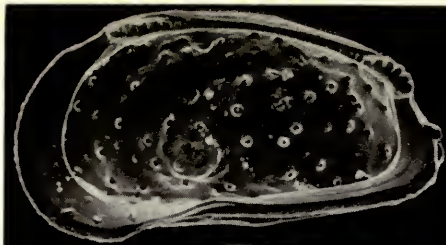
FIG. 5. *Finmarchinella* (*B.*) *barentzovoensis* (Mandelstam). Female left valve, HU. 80.R.24. External lateral view. Russian Harbour, Novaya Zemlya.

FIG. 6. *Finmarchinella* (*F.*) *finmarchica* (Sars). Male left valve, B.M. No. M.3287 A. a. External lateral view. b. Oblique anterior view. Holsteinsborg Harbour, Greenland.

FIG. 7. *Finmarchinella* (*F.*) *finmarchica* (Sars). Female left valve, B.M. No. M.3287 B. a. External lateral view. b. Oblique anterior view. Holsteinsborg Harbour, Greenland.

FIG. 8. *Finmarchinella* (*B.*) *angulata* (Sars). Female left valve, Oslo Museum F 1447.4. a. External lateral view. b. Oblique anterior view. Locality unknown.

FIG. 9. *Finmarchinella* (*B.*) *barentzovoensis* (Mandelstam). Female left valve, HU. 80.R.25. Oblique anterior view. Russian Harbour, Novaya Zemlya.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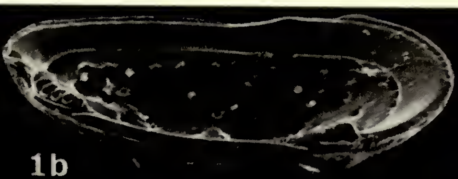
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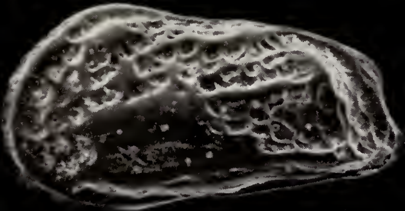
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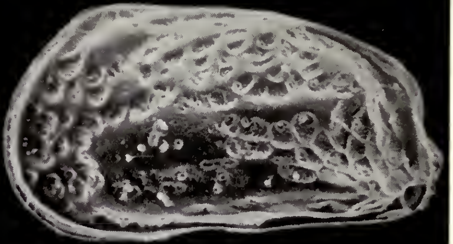
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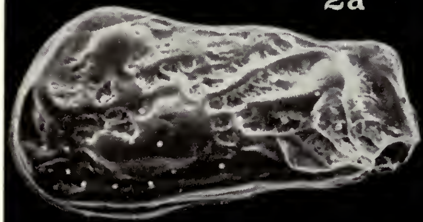
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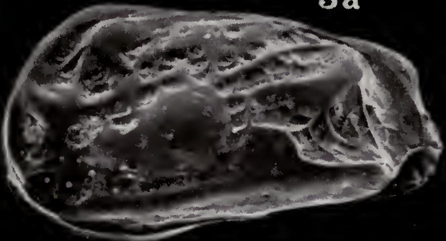
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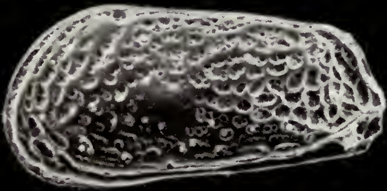
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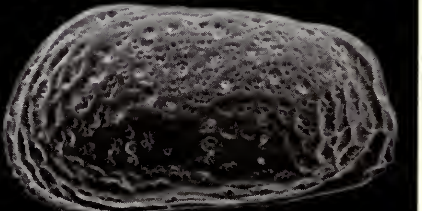
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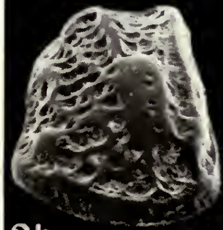
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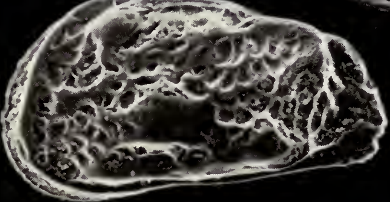
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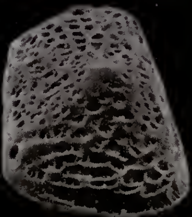
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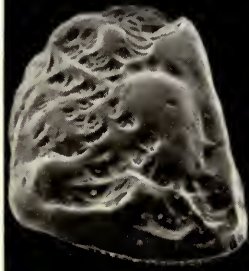
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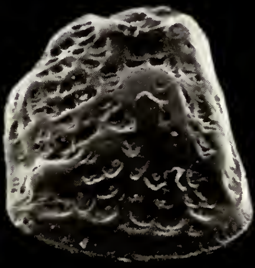
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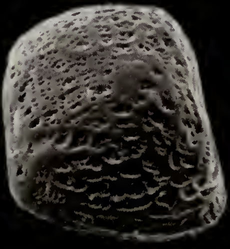
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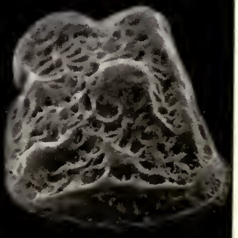
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PLATE 2

Finmarchinella

FIG. 1. *Finmarchinella (F.) finmarchica* (Sars). Male carapace, B.M. No. M.3287 C. Dorsal view. × 74. Holsteinsborg Harbour, Greenland.

FIG. 2. *Finmarchinella (B.) angulata* (Sars). Male carapace, B.M. No. 1973.331. Dorsal view × 74. Holsteinsborg Harbour, Greenland.

FIG. 3. *Finmarchinella (B.) curvicosta* sp. nov. Paratype. Female carapace, B.M. No. 1973.314. Dorsal view × 73. Holsteinsborg Harbour, Greenland.

FIG. 4. *Finmarchinella (B.) angulata* (Sars). Female carapace, B.M. No. 1973.332. Dorsal view × 72. Holsteinsborg Harbour, Greenland.

FIG. 5. *Finmarchinella (F.) finmarchica* (Sars). Female carapace, B.M. No. M.3287 D. Dorsal view × 74. Holsteinsborg Harbour, Greenland.

FIG. 6. *Finmarchinella (B.) angulata* (Sars). Female right valve, Oslo Museum No. F 1447.6. Internal view showing muscle scar pattern × 335. Locality unknown.

FIG. 7. *Finmarchinella (B.) curvicosta* sp. nov. Female left valve, HU. 80.R.26. External lateral view × 60. Russian Harbour, Novaya Zemlya.

FIG. 8. *Finmarchinella (B.) curvicosta* sp. nov. Paratype. Female right valve, B.M. No. 1973.312. a. Anterior part of hinge × 160. b. Posterior part of hinge × 160. Holsteinsborg Harbour, Greenland.

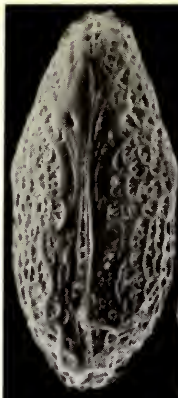
FIG. 9. *Finmarchinella (B.) curvicosta* sp. nov. Paratype. Female left valve, B.M. No. 1973.313. Oblique ventral view × 62. Holsteinsborg Harbour, Greenland.

FIG. 10. *Finmarchinella (B.) angulata* (Sars). Female left valve, Oslo Museum No. F 1447.4. Lateral view of posterodorsal part of valve × 160. Locality unknown.

FIG. 11. *Finmarchinella (F.) finmarchica* (Sars). Female left valve, B.M. No. 3287 B. Lateral view of posterodorsal part of valve × 144. Holsteinsborg Harbour, Greenland.

FIG. 12. *Finmarchinella (B.) barentzovoensis* (Mandelstam). Female left valve, HU. 80.R.25. Lateral view of posterodorsal part of valve × 144. Russian Harbour, Novaya Zemlya.

FIG. 13. *Finmarchinella (B.) curvicosta* sp. nov. Holotype. Female left valve (of carapace), B.M. No. 1973.310. Lateral view of posterodorsal part of valve × 135. Holsteinsborg Harbour, Greenland.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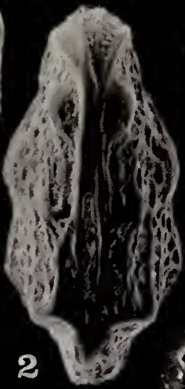
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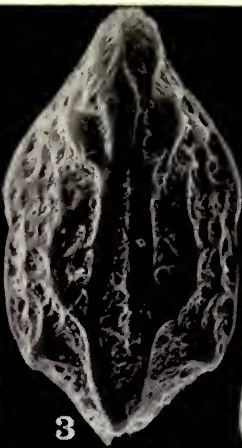
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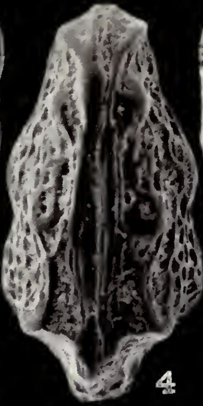
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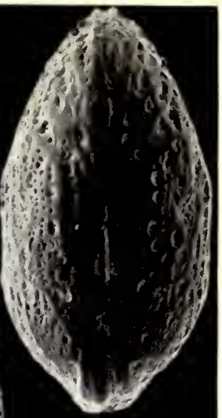
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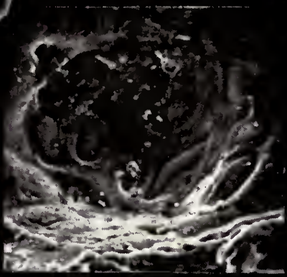
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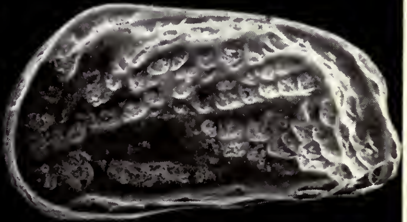
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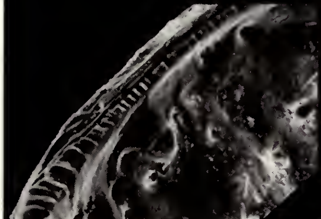
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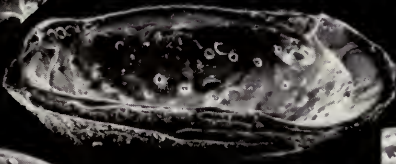
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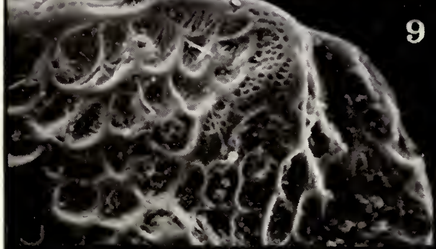
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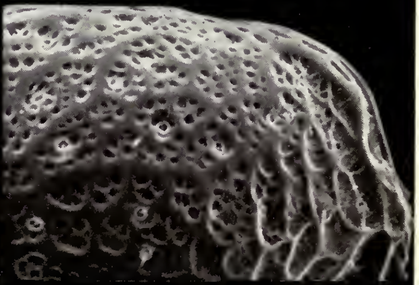
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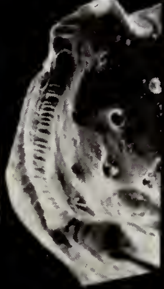
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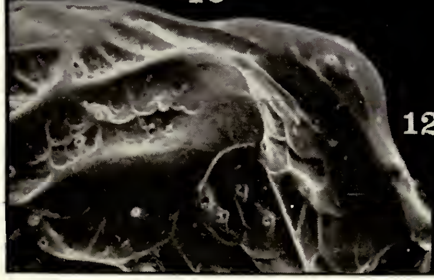
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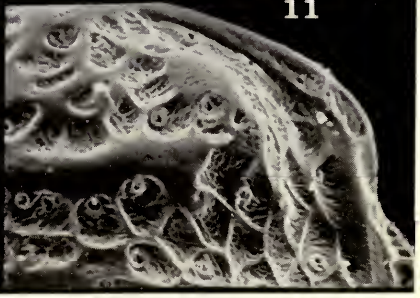
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EUPLOTES RARISETA SP. N. (PROTOZOA: CILIATEA) A NEW SMALL MARINE HYPOTRICH

By C. R. CURDS, B. JEAN WEST & JEAN E. DORAHY

INTRODUCTION

TUFFRAU (1960) listed 55 specimens of the genus *Euplotes* Ehrenberg, 1830 that had been described to that date, and in his extensive revision of the genus eliminated many of the species. In doing so, Tuffrau (1960) suggested that there were four characters of fundamental importance which should be used for taxonomic purposes at the species level. These characters were: the number of laterodorsal kineties, the arrangement of the dorsal silver-line network, the number of frontoventral cirri and the shape of the non-dividing macronucleus. Borror (1968) added the appearance of the pellicular or cortical sculpturing that is often a feature of some *Euplotes* spp. as a further criterion. Using these characters, in addition to some of the more traditional features, Borror (1972) listed 43 species of *Euplotes* in his revision of the order *Hypotrichida* Stein, 1859.

When both traditional and modern criteria are considered, the species of *Euplotes* described in the present paper does not conform to any of those listed by Borror (1972) nor Carter (1972).

MATERIALS AND METHODS

(a) *Source and cultivation*

The hypotrich was originally contained in a sample of seawater collected from Aberystwyth, Wales. Some seawater was inoculated into a flask of Erdschreiber solution ('Medium 1', Committee on Cultures, Society of Protozoologists, 1958) which was then incubated in the dark at room temperature (about 20 °C) for several weeks. Under these conditions, *Euplotes* was the dominant ciliate which grew. Some of the cells so obtained were used by Miss Sheila Andrews to initiate a culture at the Cambridge Culture Centre of Algae and Protozoa (*Euplotes* sp. LB 1624/2a). Later, a clonal culture was established (*Euplotes* sp. LB 1624/2b) and most of the work described herein relates to that clone.

The hypotrich was maintained in the dark at room temperature in conical flasks or test tubes containing Erdschreiber solution. Cultures were fed weekly with a few drops of a thick suspension of freeze-dried baker's yeast and subcultured at monthly intervals. The ciliate also grew well in 150 ml conical flasks containing 100 ml of seawater and 10–12 rice grains, but the maximum populations reached in these cultures were lower than those achieved by the former culture method. In order to establish the possible ecological range of this species, some experimental work was carried out with media consisting of various dilutions of Erdschreiber solution supplemented with baker's yeast and seawater supplemented with rice grains. In these

Bull. Br. Mus. nat. Hist. (Zool.) **27**, 2

experiments, duplicate cultures in each medium were subcultured serially into flasks containing media of progressively lower salinity at 10 per cent (v/v) intervals. The inoculum size was always 4 ml per 100 ml of medium and a period of 1–5 weeks at room temperature was allowed between each transfer. In this way it was possible to establish the approximate lower salinity limit for this species.

(b) *Light microscopy*

Observations and measurements were made using both living and fixed material. Living organisms were slowed by immersion in methyl cellulose (5 per cent w/v in seawater), and osmium tetroxide vapour (2 per cent w/v) was found to be a suitable fixative for cells which were to be drawn or measured. Large numbers of *Euplotes* were fixed in bulk and their nuclei were stained using Dippell and Chao's modification of De Lamater's basic fuchsin stain (Sonneborn, 1950). The silver-line system was displayed using the 'wet' method modified by Chatton & Lwoff (1930) and Corliss (1953).

(c) *Scanning-electron microscopy*

The preparation of these marine organisms for the scanning-electron microscope proved to be rather more complex than the method described by Small and Marszalek (1969). It was found necessary to wash the cells 5 or 6 times prior to fixation in order to separate the cells from bacteria, yeast and débris. The first two washes were carried out by slow centrifugation (approx. 400 *g*) for a few seconds. In this case the majority of the *Euplotes* were retained in the supernatant. The cells were then repeatedly washed in membrane-filtered seawater and centrifuged at approximately 1750 *g*. The cells in the final pellet were rapidly killed in osmium tetroxide vapour to prevent the cirri curling during fixation. Considerable effort was made to find a good method of fixation for these marine ciliates which was suitable for scanning-electron microscopy. The fixative suggested by Small & Marszalek (1969) was that used by Parducz (1967) and although this was acceptable in some respects, it had the disadvantage of disrupting the structure of the cirri and the adoral zone of membranelles (AZM). The fixative finally chosen, although it is still under review, consisted of equal parts of 2 per cent (w/v in distilled water) osmium tetroxide and a saturated aqueous solution of mercuric chloride. Sufficient sodium chloride was then added to give a final concentration of 3·3 per cent (w/v) ; this prevented the cells swelling during fixation. The three component parts were mixed immediately before use and then membrane filtered ; cells were fixed in the filtered solution overnight. Following fixation, the cells were washed repeatedly (at least 8 times) in membrane-filtered triple glass-distilled water and centrifuged at approximately 400 *g* between each wash. The washed cells were then frozen by being dropped onto pieces of aluminium floating on liquid nitrogen and were dried in a tissue dryer essentially as described by Small & Marszalek (1969). The pieces of aluminium covered with organisms were glued to stubs and coated with approximately 100 Å of gold as described by Harris, Martin & Ogden (1972), specimens were examined with a Cambridge 'Stereoscan' Mk II scanning-electron microscope (Cambridge Instruments Ltd, Cambridge, England).

Euplotes rariseta sp. n.

Diagnosis

Small (30–45 μm long, 20–31 μm wide), ovoid, marine hypotrich with 10 frontoventral, 5 transversal and 3 caudal cirri ; caudal cirrus below AZM stout. Ventral surface heavily sculptured with 6 posteriorly projecting ridges. Dorsal surface with 6 double-edged longitudinal ridges. Dorsal bristles sparse ; 6 kineties with a maximum of 6 bristles in the central kineties. Dorsal silver-line system double of the *patella* type. Macronucleus S-shaped. Micronucleus small, situated anteriorly.

Type slides showing silver-line systems, nuclear apparatus and whole mounts have been deposited in the slide collection of the Protozoa Section, BM (NH) : holotype Reg. No. 1972:11:1:11 ; paratype Reg. Nos. 1972:11:1:12–18.

Body size and shape

The size distribution data of *Euplotes* cells at the stationary and logarithmic phases of growth are given in Fig. 1. It should be noted that *Euplotes* cells from the logarithmic phase are considerably larger (42 ± 3 μm long by 28 ± 3 μm wide) than are cells from the stationary phase (34·6 ± 3 μm long by 24·2 ± 2·3 μm wide). This is in agreement with the observations of Curds & Cockburn (1971) who noted that the size of the ciliate *Tetrahymena pyriformis* was related to its rate of growth. The data on size show that this species of *Euplotes* is amongst the smallest recorded for the genus.

The dorsal surface is conspicuously sculptured with 6 double-edged longitudinal ridges (Pl. 1, figs. a and c). To the left of each ridge is a parallel row of pits from which the short (2 μm long) dorsal cilia or bristles emerge. The ventral surface is also strongly sculptured (Fig. 2 ; Pl. 1, figs. a and c), particularly in the posterior region between the transverse cirri. There are 6 ventral ridges, 3 of which are prominent and consist of an oblique midventral ridge, and 2 ridges which run longitudinally flanking the 2 outermost transverse cirri. The other 3 ridges are less prominent and are more or less restricted to the area immediately between the transverse cirri. All 6 ventral ridges project slightly posteriorly between the transverse cirri and form fin-like structures (Fig. 2 ; Plate 1, figs. b and c). The right buccal overture has a slight anterior evagination as in *Euplotes alatus* Kahl, 1932 (see Borror, 1968) but in the species under description it extends only just past the AZM.

Ciliary organelles

This *Euplotes* has 10 frontoventral cirri which are arranged as shown in Pl. 1, fig. b and in Figs. 2 and 3b. The arrangement closely resembles that of both *Euplotes charon* Ehrenberg, 1830 and *Euplotes quinquecarinatus* Gelei, 1950 (see Borror, 1968). There is the normal complement of 5 transverse cirri which arise between the ventral ridges and these, particularly cirri III 1 and IV 1 (following the numeration of Wallengren, 1900), are frequently seen to be frayed at the distal end (Fig. 2). The tendency for the transverse cirri to disrupt in this way is greatly increased during fixation. There are only 3 caudal cirri, and in this species the one

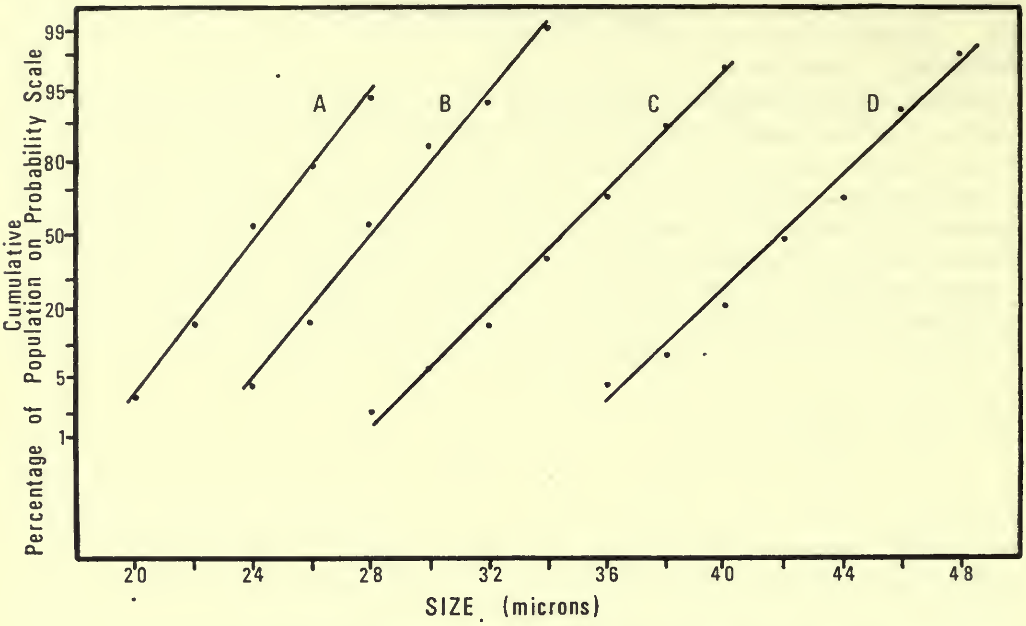

FIG. 1. Size distribution data of *Euplotes rariseta*. Curve A. Breadth of cells at stationary phase. Curve B. Breadth of cells during logarithmic growth. Curve C. Length of cells at stationary phase. Curve D. Length of cells during logarithmic growth. Stationary-phase cells were fixed in osmic acid vapour. Logarithmic-phase cells were measured alive immersed in methyl cellulose solution.

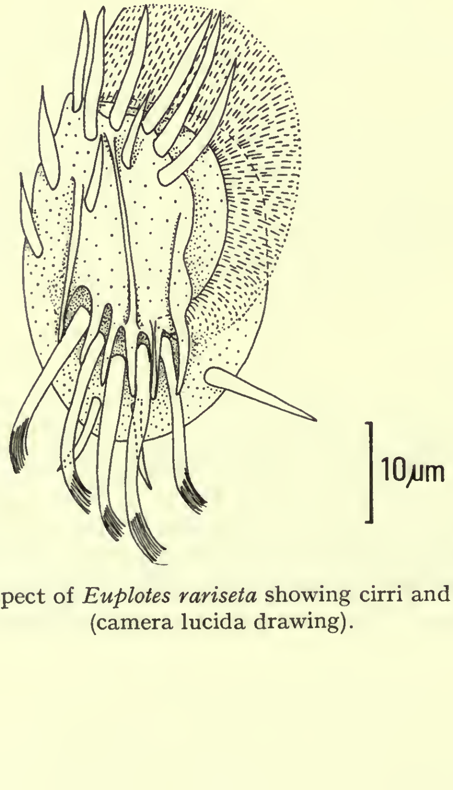

FIG. 2. Ventral aspect of *Euplotes rariseta* showing cirri and ventral ridges (camera lucida drawing).

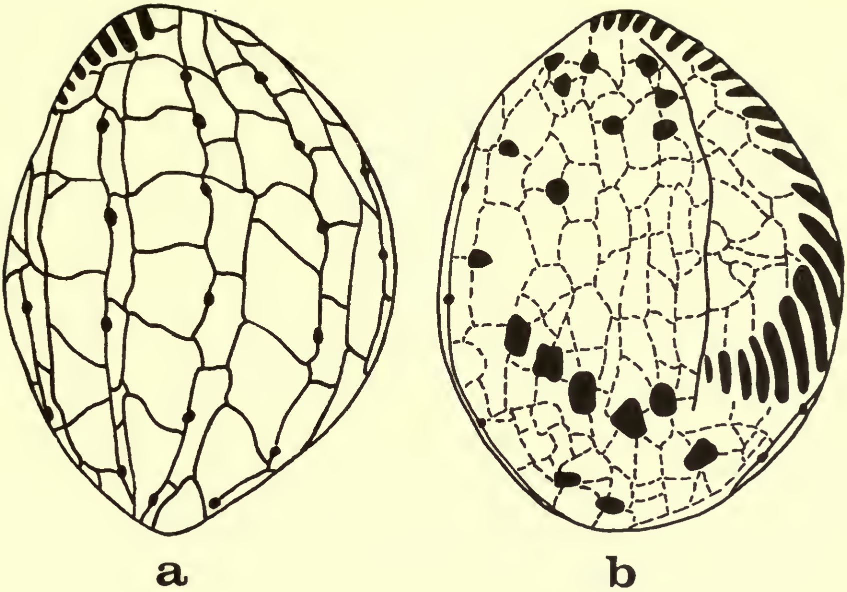

FIG. 3. Silver-line system of *Euplotes rariseta*, (a) dorsal surface, (b) ventral surface.

below and nearest to the AZM is characteristically held stiffly out to the left side and is much stouter than the other two caudal cirri which arise beneath the central transverse cirri (Fig. 2). The presence of this large stiff caudal cirrus appears to be a feature unique to this species ; in the living cell, the cirrus seems to act as a rudder-like structure. The dorsal bristles are sparse in this species ; there are 6 rows and the mid-dorsal rows have only 6 bristles, in which respect this species resembles *Euplotes bisulcatus* Kahl, 1932 (see Borror, 1968).

Nuclei

The macronucleus of this species is an irregular S-shape (Fig. 4). In this respect it appears to be unique in the genus *Euplotes*. The posterior part of the macronucleus points anteriorly and ventrally towards the position of the cytostome. The micronucleus is situated close to the macronucleus on the left anterior edge of the body (Fig. 4).

Silver-line system

The geometry of the dorsal silver-line system is of the double or *patella*-type and closely resembles that of *Euplotes raikovi* Agamaliev, 1966 with a series of alternate longitudinal rows of narrow long polygons and wide short polygons (Fig. 3a). The ventral argyrome (Fig. 3b) consists of an irregular network of polygons in similar numbers to that of *E. cristatus* Kahl, 1932 (see Tuffrau, 1960). The dorsal silver-line network has been seen on some scanning-electron micrographs (Pl. 1, fig. d).

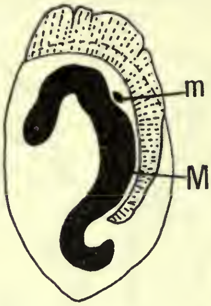

FIG. 4. Ventral view of the nuclei of *Euplotes rariseta* from a stained preparation. (M = macronucleus, m = micronucleus.)

Ecological data

Cells inoculated into Erdschreiber solution supplemented with yeast grew well in nine different dilutions of this medium from 100 down to 20 per cent (v/v). Cells transferred from 20 to 10 per cent Erdschreiber solution showed no growth during the 6 weeks following inoculation. Growth in seawater supplemented with rice grains was good in seven dilutions from 100 down to 40 per cent (v/v), but cells transferred from 40 to 30 per cent seawater showed good growth only after 3 weeks in culture. Subsequent transfer of cells from 30 to 20 per cent seawater led to poor growth after 5 weeks, and no growth was observed in 10 per cent seawater. Contractile vacuole activity was not observed in organisms from any of the tested dilutions of seawater or Erdschreiber solution. This is in agreement with the findings of Yocum (1934), who found that the activity of the contractile vacuole in *Euplotes patella* Ehrenberg, 1831 diminished and became imperceptible at concentrations of seawater above 10 per cent. Yocum (1934) also found that *E. patella* would survive well and divide in 66 per cent seawater. In view of the finding that the species of *Euplotes* described in the present paper will survive and divide in dilutions of seawater or Erdschreiber solution between 20 and 100 per cent, it seems likely that, in nature, this organism could be found in both marine and brackish environments. However, for the lower dilutions tested, organisms were not as abundant in seawater medium as they were in Erdschreiber medium, and it is possible that in these experiments the amounts of substances other than sodium chloride were limiting growth.

DISCUSSION AND CONCLUSIONS

In the past, some authors have noted that the number of caudal cirri is not as constant as the others, for example, *Euplotes mutabilis* Tuffrau, 1960 has 4–5 caudals, *E. raikovi* has 2–3 caudals and there are other similar examples. In view of these observations perhaps the use of the number of caudal cirri as a character should be regarded with caution. Although *E. octocirratus* Agamaliev, 1967 is the only other species of *Euplotes* which has precisely the same numbers of cirri on the ventral surface, that is 10 frontoventrals, 5 transversals and 3 caudals, one should consider those species with a 10 : 5 : 4 cirri complement. These include the following: *E. alatus*, *E. balteatus* Kahl, 1932, *E. crenosus* Tuffrau, 1960, *E. cristatus*, *E. harpa* Stein, 1859, *E. indentatus* Carter, 1972, *E. inkystans* Chatton in Tuffrau, 1960, *E. minuta* Yocum, 1930, *E. magnicirratus* Carter, 1972, *E. quinquecarinatus*, *E. roscoffensis* Dragesco, 1966, *E. trisulcatus* Kahl, 1932, *E. tuffraui* Berger, 1965 and *E. vannus* Minkjewicz, 1901. In all these species the shapes of the macronuclei are quite unlike that of the species described in this paper and furthermore the silver-line systems of these species are different.

It is unfortunate that the dorsal and ventral silver-line systems have not been described for all the known species of *Euplotes* ; however, of those listed above none have 6 dorsal kineties as found in *E. rariseta* ; only *E. octocirratus* and *E. trisulcatus* have 7 kineties, the remainder have 8 or more. There are four other species with 6 dorsal kineties and these are *E. raikovi*, *E. strelkovi* Agamaliev, 1967, *E. tegulatus* Tuffrau, 1960 and *E. balticus* Kahl, 1932. None of these four species have the correct numbers of cirri and furthermore all possess far too many dorsal kinetosomes. *E. bisulcatus* is the only other species with a maximum of 6 dorsal kinetosomes per kinety but there are 8 dorsal kineties in that species.

Euplotes rariseta differs from all previously described species of *Euplotes* in possessing an S-shaped macronucleus and a very stout caudal cirrus. In addition, although the remaining characters have been observed amongst other species of *Euplotes*, it is evident from the information given above that none of these species has the same combination of characters. For these reasons, it is considered that the species of *Euplotes* described in this paper is sufficiently distinct from all others to be designated as a separate species, and because of the paucity of dorsal bristles has been named *Euplotes rariseta*. Following the revised classification of the Committee on Taxonomic Problems of the Society of Protozoology (Honigberg *et al.* 1964) *Euplotes rariseta* is placed into class Ciliatea Perty, 1852, order Hypotrichida Stein, 1859, family Euplotidae Ehrenberg, 1838.

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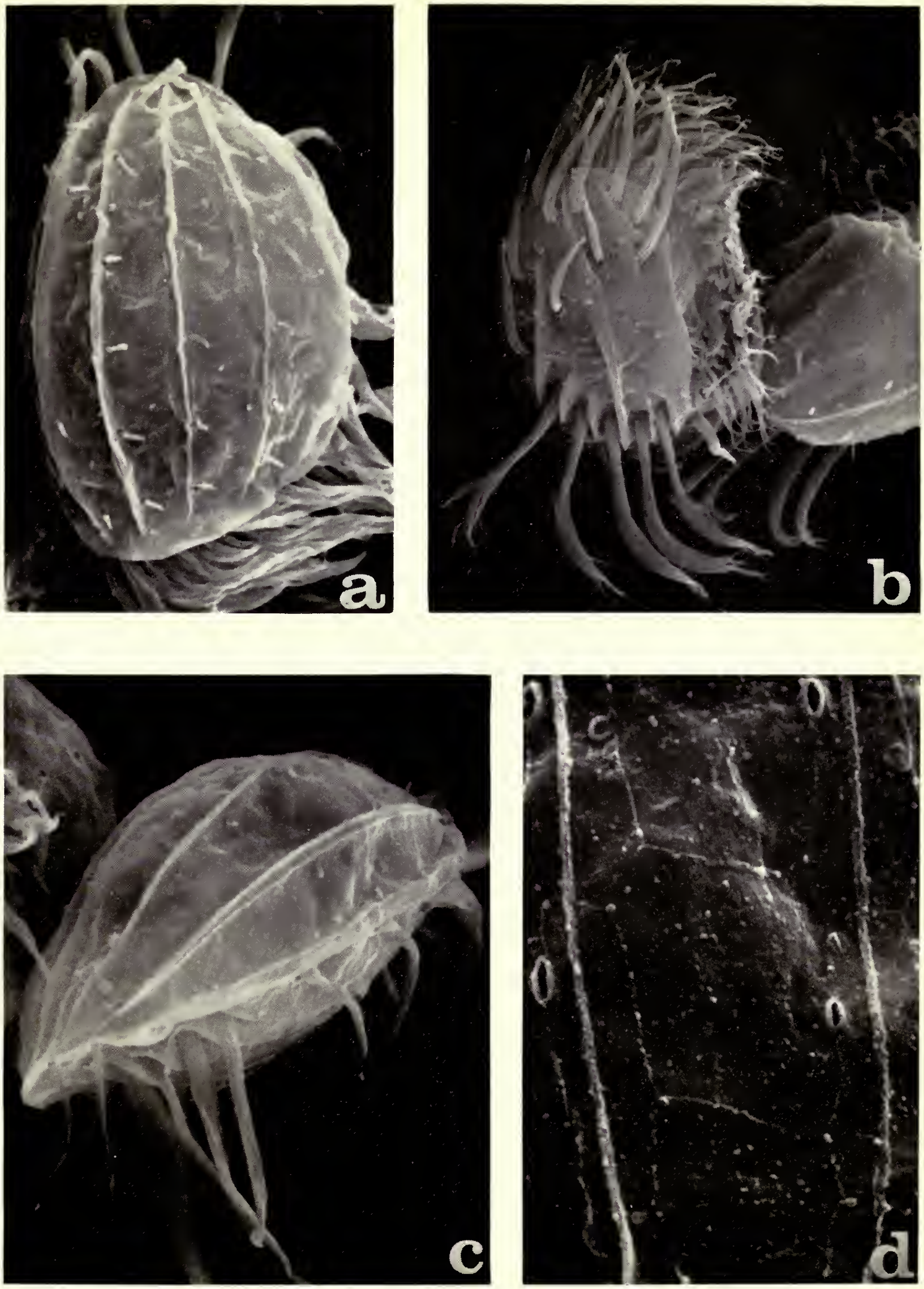
PLATE 1

Scanning micrographs of *Euplotes variseta*

a. Dorsal view showing ridges and rows of dorsal bristles (× 2·1k)
b. Ventral view showing the arrangement of cirri and ventral ridges (× 1·8k)
c. Posterolateral aspect showing double-edged dorsal ridges (× 2·7k)
d. Dorsal surface showing argyrome (× 6·1k)


a
b
c
d

OBSERVATIONS ON CLONAL CULTURES OF *EUGLYPHA ACANTHOPHORA* AND *EUGLYPHA STRIGOSA* (TESTACEA: PROTOZOA)

By R. H. HEDLEY, C. G. OGDEN & JUNE I. KRAFFT

INTRODUCTION

MANY testate amoebae are known only from their original descriptions, based on observations made at the magnification limits of the optical microscope. The introduction of scanning-electron microscopy for surface ultrastructure examination now allows more accurate descriptions to be made of these animals. The present account describes the shell morphology and biology of two species of *Euglypha* Dujardin, 1841, namely *Euglypha acanthophora* (Ehrenberg, 1841) and *Euglypha strigosa* (Ehrenberg, 1871), both of which have been recently isolated from samples of sewage sludge and moss respectively, collected in southern England. This is the third paper in a series dealing with testate amoebae. The previous papers (Hedley and Ogden, 1973, 1974) are devoted to the biology and fine structure of *Euglypha rotunda* and *Trinema lineare* respectively. Fine structure observations on the cytoplasm of *E. acanthophora* and *E. strigosa* will be the subject of a separate publication.

The genus *Euglypha* belongs to the family Euglyphidae – the classification adopted here is that proposed by Loeblich and Tappan (1961):

Class	*RHIZOPODEA*	Von Siebold, 1845
Subclass	*FILOSIA*	Leidy, 1879
Order	GROMIDA	Claparède and Lachmann, 1859
Superfamily	**EUGLYPHACEA**	Loeblich and Tappan, 1961
Family	**EUGLYPHIDAE**	Wallich, 1864 test hyaline, symmetrical, elongate, composed of rounded siliceous scales, aperture rounded or elongate; one nucleus.

Previous work – biology

Euglypha acanthophora. Most of the early biological observations of *Euglypha* were made on this species. These reports (Leidy, 1877; Gruber, 1881; Blochmann, 1887; Schewiakoff, 1888; Carter, 1889; Penard, 1890; Reukauf, 1912; Popoff, 1912) dealt mainly with nuclear division and reproduction by binary fission. Carter (1865, 1889), Reukauf (1912) and Popoff (1912) also described another process of division in which many individuals were produced at one time, but all the stages of this division were not seen. A report by Jones (1929), made from observations on an old protozoan culture, described a flagellate stage for *E. acanthophora*. This has not been confirmed and it is possible that the cultures were contaminated.

Encystation was observed by Penard (1890, 1902), Leidy (1879), Popoff (1912) and Reukauf (1912). Leidy (1879) described the cyst as being enclosed in two distinct envelopes, and Popoff (1912) illustrated the various stages in the process of encystation. When two individuals were observed joining to form a single large specimen and immediately formed a cyst, Reukauf (1912) suggested that this was a copulation cyst which at excystation produced many new individuals.

In studies on the distribution of testaceans in relation to their habitats, Heal (1961) found *E. acanthophora* in small numbers associated with fen areas, whereas de Graaf (1956) considered this species to have no particular associations.

Euglypha strigosa. This species has been recorded from both wet and dry habitats. de Graaf (1956) noted that in a Netherland fen it preferred drier *Sphagnum*, whilst Heal (1961) described it as a eurytopic species occurring in large numbers in bog hummocks in Northern England and also noted (Heal, 1962) that it appeared to be restricted to the lower levels of the *Sphagnum*. Differences in shell size and shape of specimens of *E. strigosa* were described by Chardez and Leclercq (1963), who suggested that these differences could be related to the type of habitats in which they occur.

Previous work – taxonomy

In a review of the *British Freshwater Rhizopoda* fauna Cash *et al.* (1915) summarize previous taxonomic reports of both *Euglypha acanthophora* and *E. strigosa*. The present account excludes these references and is restricted to subsequent descriptions.

Euglypha acanthophora (Ehrenberg, 1841). This species was originally described as *E. alveolata* but was made a synonym of *E. acanthophora* by Cash *et al.* (1915) who gave a detailed account of their reasons, and this has since been accepted by most authors. They (Cash *et al.* 1915) redescribed *E. acanthophora* and also two varieties which differed mainly in size, and the shape and number of the elongated shell-plates. Further redescriptions and sizes were given by Hoogenraad and de Groot (1940) and Decloitre (1962, 1965), the latter author also described (Decloitre, 1962) seven varieties of *E. acanthophora*.

Euglypha strigosa (Ehrenberg, 1872). Cash *et al.* (1915) described this species as 'the most generally distributed and numerous of the *Euglyphae*', easily distinguished from *E. ciliata* and *E. compressa* by its thickened apertural-plates and circular aperture. In a review of the genus *Euglypha*, Decloitre (1962) redescribed *E. strigosa* and three varieties. Additional sizes and descriptions were given by Bartŏs (1963) and Decloitre (1964). The surface ultrastructure of the shell of *E. strigosa* was described by Cambar *et al.* (1964), from metal and carbon-shadowed preparations.

MATERIALS AND METHODS

Euglypha acanthophora was isolated from a sample of sewage sludge from Maple Lodge Works of the Colne Valley Sewage Board, Hertfordshire, in December, 1972.

Euglypha strigosa was isolated from a sample of sphagnum moss collected in the New Forest, near Christchurch, Hampshire, in April, 1970. Both species were obtained from crude cultures made from small portions of each type of material placed in a shallow layer of culture liquid and kept in the laboratory at room temperature, 18–20 °C. Agnotobiotic cultures were kept in small plastic containers, on a thin layer of agar agar (1 per cent in distilled water) with a sterilized wheat grain added prior to setting and covered with a shallow layer of culture liquid. The culture liquid was a 5 per cent (w/v) solution of soil extract, plus 100 mg/l^{-1} sodium nitrate and 15 mg/l^{-1} sodium dihydrogen orthophosphate, in distilled water. *E. strigosa* has more recently been kept on 1·5 per cent agar in amoeba saline, with a sterilized rice grain added and covered with a shallow layer of Prescott and James solution (Prescott & James, 1955).

Clonal cultures were established by isolating single active animals. One clone has been used subsequently to produce the working cultures of each species. These clones have been deposited, *E. strigosa* (No. 1520/2), *E. acanthophora* (No. 1520/3), and maintained at the Culture Centre of Algae and Protozoa, The Natural Environment Research Council, Cambridge, England. Subcultures made at 4–5 week intervals are adequate to maintain active animals that readily feed and reproduce.

Optical microscopy. Specimens were examined by both phase-contrast and bright-field illumination, either live or after fixation with Schaudinn's fluid. Smears of fixed animals were stained with either borax carmine or iron haematoxylin.

Scanning-electron microscopy. Live specimens were either cleaned by transferring them from the culture vessels through several changes of triple-distilled water, or fixed in glutaraldehyde and then thoroughly washed. They were then manipulated using a single-hair brush onto a small cover-slip, previously cleaned with acetone and lint-free tissue, to which they adhere when dry. To obtain single siliceous shell-plates, an individual clean specimen was placed on a small segment of cover-slip and covered with a small drop of concentrated sulphuric acid. This was heated gently to evaporate the acid and liberate the plates from the organic cement. These prepared cover-slips were secured to 'Stereoscan' stubs with an electrically conductive paint, 'Silver Dag', prior to being coated evenly with 10–15 nm of gold using the method recommended by Harris *et al.* (1972). The stubs were examined on either the Cambridge Stereoscan Mk II or Stereoscan 600, operating at 15 or 20 kV and the results were recorded on Ilford HP4 film.

DISTRIBUTION

E. acanthophora is usually found in damp mosses, submerged vegetation and standing water, whilst *E. strigosa* is found in similar habitats and additionally in drier mosses and soil.

A full list of locality records and references was given by Decloitre (1962). Since this review several authors, namely, Bartŏs (1963), Bonnet (1966), Decloitre (1964, 1965) and Stĕpánek (1963), have recorded these species from other localities and these are included here.

The following lists illustrate the geographically widespread distribution of both species :

Euglypha acanthophora

Europe : England, Wales, Scotland, Ireland, France, Holland, Belgium, Germany, Spain, Switzerland, Hungary, Czechoslovakia, Luxembourg, Iceland and Lapland.
North America : Greenland, Canada and the United States of America.
South America : Venezuela and Colombia.
Africa : Congo, Cameroons, French West Africa, South Africa and Madagascar.
Asia : China, Japan, Java and Sumatra.
Australasia : Australia and New Zealand.

Euglypha strigosa

Europe : England, Wales, Scotland, Ireland, France, Belgium, Holland, Spain, Germany, Switzerland, Italy, Hungary, Czechoslovakia, Bulgaria, Rumania, Spitzbergen, Finland and Iceland.
North America : Greenland, Canada and the United States of America.
South America : Central America, Colombia, Venezuela and Chile.
Africa : South Africa, French West Africa, Madagascar and the Canary Islands.
Asia : Krakatoa Island, Borneo and Java.
Australasia : Australia, Tasmania and New Zealand.
Antarctica : Adelaide Island.

MORPHOLOGY AND VARIATION

Euglypha acanthophora. The shell has a mean length of 70·8 μm ±9·6 μm and a mean breadth of 39·0 μm ±4·4 μm ; it is elliptical in shape through the major axis and circular through the minor axis (Pl. 1, fig. A), and is made up of three different types of siliceous plates – apertural-plates (Pl. 1, fig. E), shell-plates (Pl. 1, fig. B) and elongated shell-plates (Pl. 1, fig. B). The aperture is terminal, circular and has a mean diameter of 18·4 μm ±4·9 μm, it is surrounded by between 10 and 13 evenly spaced apertural-plates (Pl. 1, fig. D). Each apertural-plate is roughly circular in shape and varies in size from 8·1 μm to 12·5 μm in length and 7·2 μm to 11·4 μm in width. The dentate edge of the apertural-plate is slightly thickened and carries a median tooth with either four or five smaller lateral teeth on each side (Pl. 1, figs. C and E). The apertural-plates are found not only bordering the aperture, but are also seen in the second and third row inside the aperture (Pl. 1, fig. E). There are approximately 200 shell-plates which range in size from 10·9 μm to 12 μm in length and 7·9 μm to 9·1 μm in width. They are roughly circular in shape with the anterior edge usually having three small pointed projections (Fig. 1a), and are arranged regularly in alternate longitudinal rows (Pl. 1, fig. A). In the posterior

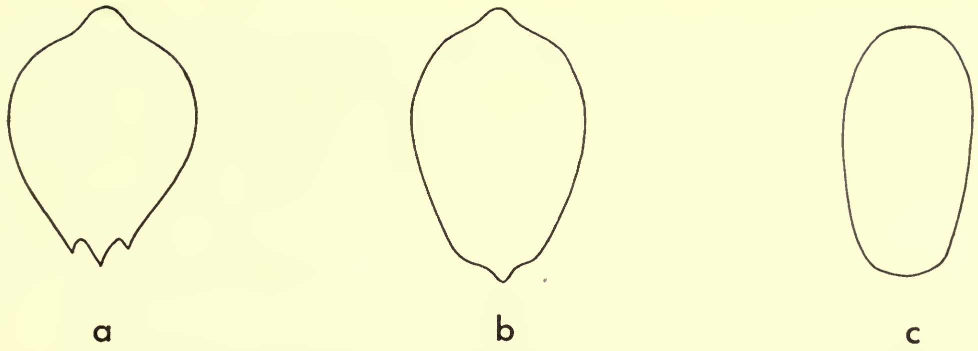


FIG. 1. Diagram to show the comparative shape of shell-plates (a) *E. acanthophora* from anterior region, (b) *E. acanthophora* from posterior region, (c) *E. strigosa*.

region of the shell there are normally between one to six elongated shell-plates which have one edge tapering to a fine point (Pl. 1, fig. B). These plates are approximately twice as long as a normal shell-plate, nevertheless, the projections break easily so that they are often seen to be short and end bluntly. The pointed edge of these elongated shell-plates is usually directed posteriorly so that they are seen to project from the outline of the shell, but on occasions they follow the curvature of the shell and are difficult to see by light microscopy.

Abnormally shaped shells occur occasionally, although the incidence of such forms appears to be less than three per cent. They are usually specimens with either deformed anterior regions or small specimens, about half or two-thirds normal length, with wide apertures. The first type is the most frequent abnormal shell form, having a normal arrangement of shell-plates in the posterior region but anterior to the middle region the shell-plates are compacted together haphazardly, so that the shell only attains half the normal length. These deformed shells usually collapse when air-dried whilst normal shells retain their shape. The animals inside these deformed shells appear to possess the normal cytoplasmic organelles.

Euglypha strigosa. The shell has a mean length of 81·3 μm ± 3·8 μm and a mean breadth of 42·2 μm ± 6 μm ; it is elliptical in shape through both the major and minor axes (Pl. 2, fig. A). Two distinct types of siliceous plates make up the shell, apertural-plates and shell-plates, and in addition there are numerous elongated siliceous spines (Pl. 2, fig. A). The aperture is terminal and circular, with a mean diameter of 14·9 μm ± 0·8 μm ; it is surrounded by between 10 and 13 evenly spaced, apertural-plates – the usual number of apertural-plates is 11 (Pl. 2, fig. E). Each apertural-plate is roughly circular in shape and varies in size from 9·2 μm to 10·8 μm in length and 7·8 μm to 8·5 μm in width. One margin is distinctly thicked and carries a large median tooth with either three or four smaller teeth on each side (Pl. 2, fig. C). The shell-plates are roughly oval in shape (Fig. 1c), with a size range of from 8·0 μm to 11·3 μm in length and 4·1 μm to 6·4 μm in width, and they are arranged in regularly spaced, alternate longitudinal rows. The thin, elongated spines vary in shape and size from small pear-shaped spines approximately 2 μm long to thin spines 23 μm long, and they project from any part of the shell surface (Pl. 1, fig. A). They are found at the junction of shell-plates, where they are held in position by a similar organic cement material to that which holds the shell-plates together in *E. rotunda* (Hedley and Ogden, 1973). This has been confirmed from the present authors unpublished observations of the fine structure of *E. strigosa*. The spines are single structures, although two or more are often seen projecting from the same junction as though they were connected. They usually project from the surface at right-angles, but they may lie close to the surface and point in any direction. There appears to be no regular arrangement in the distribution of the spines, although usually only the smaller spines are seen at the junction of the apertural-plate and shell-plate region, and the largest spines seem to lie along the lateral margins. The spines appear to be removed easily by abrasive action (Pl. 2, fig. B).

No abnormal forms of this species have been seen in our cultures.

REPRODUCTION

Euglypha acanthophora. Growth curves produced from observations made on three replicate cultures gave an estimated doubling time of between 2·3 and 2·8 days. Cytoplasmic division proceeds in a similar sequence to that previously described for *E. rotunda* by Hedley and Ogden (1973). The approximate time taken to produce the daughter shell is 25 minutes, whereas the time taken for the completion of binary fission is two hours. The animals are usually active after division with strong pseudopodial movement (Fig. 2).

Eight specimens with abnormal apertures were isolated and after six days had divided to produce 27 normal individuals. Observations on individual, dividing abnormal forms, such as those with a wide aperture and others being half normal size, show that they often produced smaller individuals with apparently the normal shell shape. One abnormal animal at division produced an almost normal shell, a small shell and some loose shell-plates (Fig. 3). Cytoplasm was present in the larger daughter shell, and the group did not separate after the normal time taken for division, but moved after this time as a group. During division in a normal individual, at the time when all the reserve shell-plates had passed into the pseudopodial trunk, a small circle of shell-plates became detached from the posterior end of the daughter shell. Binary fission proceeded normally and the two individuals separated, leaving behind the circle of shell-plates.

Euglypha strigosa. An estimated doubling time of between 3·9 and 4·3 days was obtained from growth curves produced from observations on three replicate cultures. Division is preceded by the retraction of the filose pseudopodia, followed by the extrusion of a large pseudopodial trunk and shortly after by the apertural-plates (Pl. 2, fig. D). The shell-plates are then arranged progressively until the daughter-shell is almost complete, at which point the spines are pushed out between the shell-plates with considerable movement. This continues for a short time after the shells are equal in size, but then the movement of both shell-plates and spines ceases abruptly. The time taken to produce a daughter-shell is approximately 50 minutes, with complete binary fission taking about three hours.

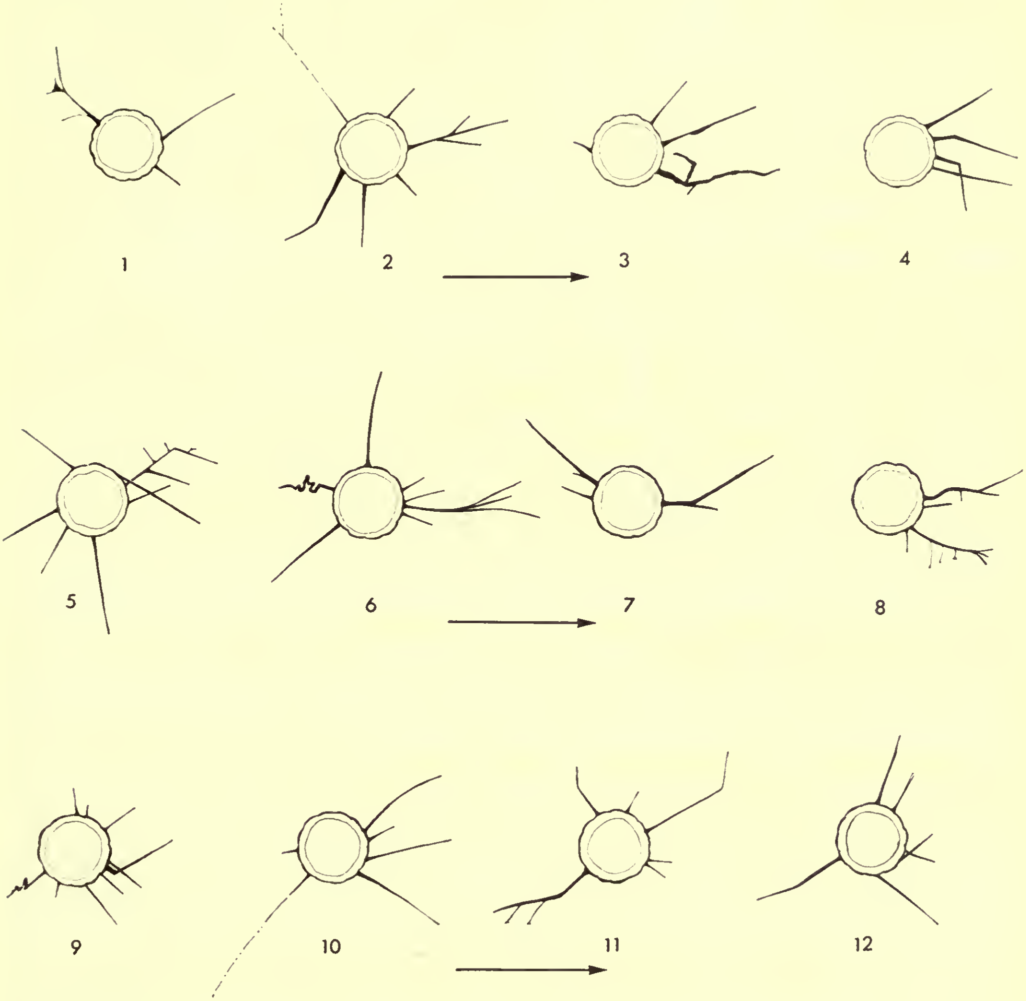


FIG. 2. Drawings of a moving specimen of *E. acanthophora* observed over a period of 30 minutes, to show the diversity of pseudopodial movement; the arrow denotes the direction of movement.

It was noted that in preparations of dividing specimens for scanning electron microscopy, the daughter-shell consistently collapsed. This is possibly due to an incomplete stabilization of the organic cement lining.

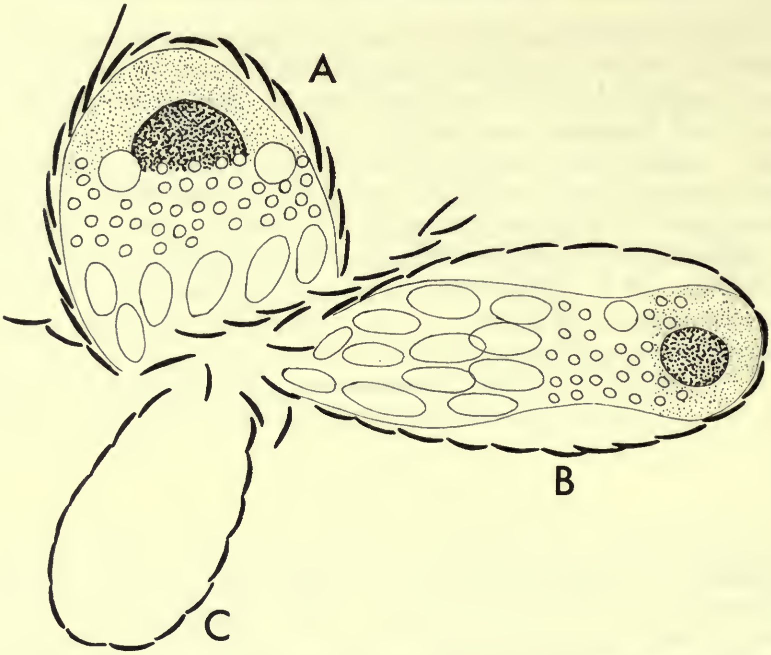


FIG. 3. Diagram representing the division products of an abnormal form ; A – abnormal form, B – apparently normal daughter and C – a small form without cytoplasm.

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PLATE 1

A. Lateral view of *E. acanthophora* showing the arrangement of the shell-plates. ×1500
B. Preparation of shell-plates to illustrate two elongated shell-plates. ×3000
C. Lateral view of single apertural-plate with characteristic teeth. ×7600
D. Aperture of *E. acanthophora* showing the arrangement of the apertural-plates. ×2900
E. Ventral view of apertural-plate preparation, to show thickened dentate edge and the arrangement of three rows of aperture-plates. ×3500

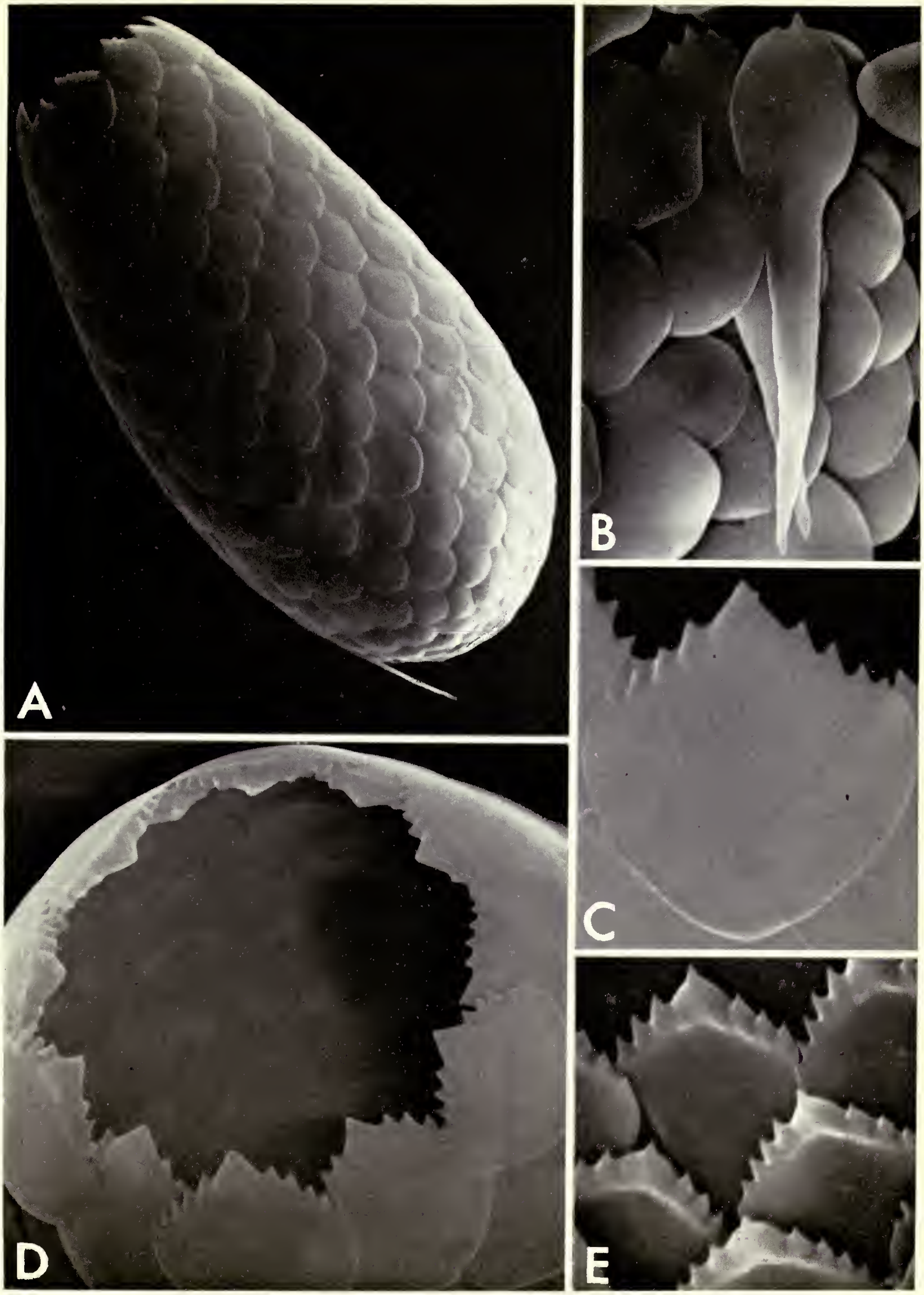
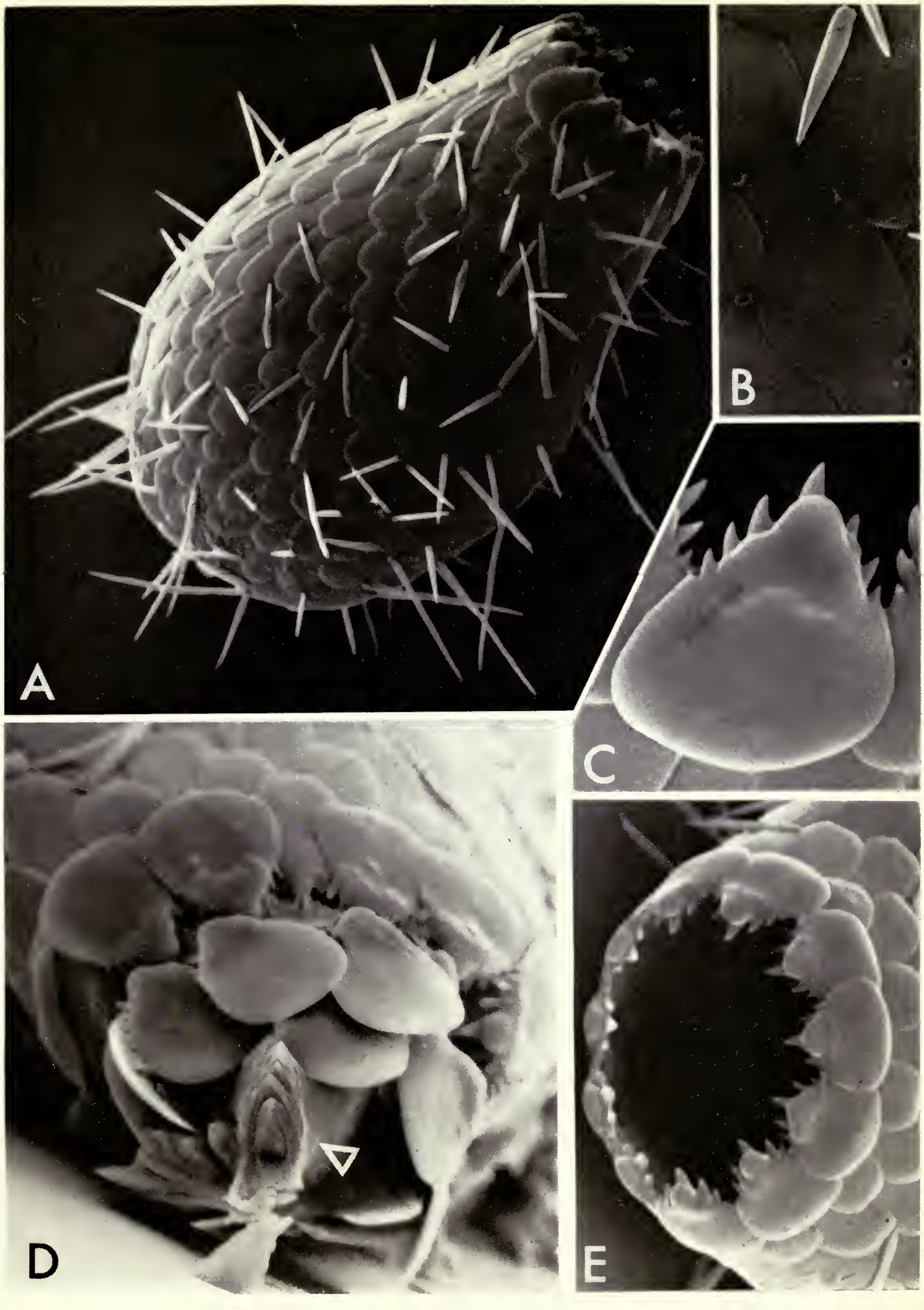

A
B
C
D
E

PLATE 2

A. Lateral view of *E. strigosa* to show the distribution of siliceous spines. ×1200
B. Area of shell surface illustrating the holes left by removal of spines. ×5000
C. Lateral view of a single apertural-plate. ×4700
D. Apertural view of the first stage of division ; note the large pseudopodial trunk (arrowed) with some daughter-shell apertural-plates arranged on it. ×2700
E. Aperture of *E. strigosa* with eleven evenly spaced apertural-plates. ×3000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DESCRIPTIONS OF THREE SPECIES OF *EUPLOTES* (PROTOZOA: CILIATEA)

By C. R. CURDS

INTRODUCTION

In his revision of the order *Hypotrichida* Stein, 1859, Borror (1972) listed 43 species of the genus *Euplotes* Ehrenberg, 1830 and in the same year Carter (1972) added a further four new species. The latter author suggested the following characters constitute a reliable basis for separating species within the genus; the pattern of the dorsal interkinetal silver-line network or argyrome, the number of dorsolateral kineties, the shape of the adoral zone of membranelles and the number of membranelles therein, the number and arrangement of the ventral cirri and the shape of the non-dividing macronucleus. Most of these characters were initially introduced by Tuffrau (1960) while Borror (1968) added the appearance of the cortical sculpturing that is sometimes a feature of the dorsal and ventral surfaces of *Euplotes* spp.

Three species of *Euplotes* are described in the present paper. The first two are freshwater forms that were isolated from samples of activated sludge and these were subsequently identified as *E. moebiusi* forma *quadricirratus* and *E. affinis* forma *tricirratus* respectively. The third is a euryhaline species from Austria which does not conform to any of those species described in the literature when both traditional and modern criteria are taken into consideration.

Euplotes moebiusi Kahl, 1932 and the variety with four caudal cirri, *E. moebiusi* forma *quadricirratus* Kahl, 1932, have not been described in the literature since their first brief descriptions and illustrations by Kahl (1932). However, this species has regularly been observed in activated-sludge plants treating sewage and industrial waste waters over many years (Curds & Cockburn, 1970; Ministry of Technology 1968). Photographs of *E. moebiusi* were published by Klein (1958) in order to demonstrate the 'dry' silver method but these were not sufficiently comprehensive for taxonomic purposes.

Euplotes affinis Dujardin, 1841 and its variety with three caudal cirri *E. affinis* forma *tricirratus* Kahl, 1932 are also examples that have not been described since their originals and yet have been seen regularly in aerobic waste-treatment processes (Curds & Cockburn, 1970) and in other organically polluted situations (Bick, 1972). Tuffrau (1960) thought it likely that both *E. moebuisi* and *E. affinis* were synonyms for the species *E. charon* Ehrenberg, 1830.

MATERIALS AND METHODS

(a) *Source and cultivation*

A clonal culture of *Euplotes moebiusi* was isolated direct from an activated-sludge sample obtained from Maple Lodge Sewage Treatment Works, Rickmansworth, Hertfordshire. This species was maintained in freshwater Erdschreiber solution

('Medium 1', Committee on Cultures, Society of Protozoologists, 1958), either in test-tubes or in Petri dishes. The largest populations were obtained in Petri dishes containing a thin layer of Musgrave and Clegg's agar (2·5 per cent agar, 0·5 per cent sodium chloride and 0·5 per cent Liebig's beef extract in distilled water) which was streaked with the bacterium *Klebsiella aerogenes* (National Collection of Industrial Bacteria, NCIB 8017) as a food supply and then flooded with Erdschreiber solution. Subcultures were transferred at monthly intervals.

Euplotes affinis was collected by Mr A. Cockburn from a sample of activated sludge taken from an experimental small-scale pilot plant operated at the Water Pollution Research Laboratory, Stevenage, Hertfordshire. It was sent to the British Museum (Natural History) as a clonal culture and was maintained in a similar manner to *E. moebiusi*.

The third hypotrich, a small euryhaline *Euplotes* sp., was originally collected by Professor E. Tschermak from a freshwater source in Schlospark Schönbrunner in Vienna which is the *locus classicus* for the alga *Ruttnera spectabilis* Geitler, 1942 (see Geitler, 1942, 1943). Samples of this alga were sent to Dr Mary Parke at the Marine Biological Station at Plymouth where the hypotrich was first noticed and cultured. Cultures of the ciliate were subsequently deposited with the NERC Culture Collection of Algae and Protozoa where it was cultivated in saltwater Erdechreiber solution. Later, a clonal culture was established in freshwater and marine media at the British Museum (Natural History) and the descriptions herein relate to organisms from that clone. This small *Euplotes* sp. could be maintained equally well in test-tubes or plastic Petri dishes containing either fresh or seawater Erdschreiber solutions. Cultures were kept in the dark at room temperature, and were fed at weekly intervals with a few drops of a thick suspension of baker's yeast. Cultures were transferred at monthly intervals.

(b) *Microscopy*

Light microscopy and the methods used for observations and measurements were similar to those described by Curds, West & Dorahy (1974). Silver-line systems were displayed using the 'wet' method of Corliss (1953) in the cases of *Euplotes affinis* and the small euryhaline species. The 'dry' method of Klein (1958) was used to show the silver-line system of *E. moebiusi*. The latter method proved to be far more reliable and quicker than the conventional 'wet' method. As Klein (1958) pointed out, the success of the 'dry' method depends on the cell drying and dying more or less simultaneously and this was achieved by removing excess moisture with the aid of screws of paper tissue and by flicking single cells out from drops of liquid onto dry parts of the slide by means of an eyelash mounted in a glass rod. Nuclei were stained using Dippell and Chao's modification of De Lamater's basic fuchsin method described by Sonneborn (1950). The nuclei of *E. moebiusi* and *E. affinis* were stained after fixation on the slide by air-drying with equal success as the conventional method of chemical fixation.

The techniques used for scanning-electron microscopy of the small euryhaline *Euplotes* sp. were similar to those previously described by Curds *et al.* (1974) with the exception of the fixation methods. Here the hypotrichs were not killed in osmium tetroxide vapour, and fixation was best using the osmium-meruric chloride fixative (Parducz, 1967) which was recommended by Small & Maraszalek (1969). A comparison of the results obtained by the fixation methods of Curds *et al.* (1974) and those of Small & Marszalek (1969) for this species is demonstrated in Pl. 1. Plate 1a shows a cell fixed in Parducz's solution following the recommendations of Small & Marszalek (1969) where Pl. 1b shows a similar cell that had been killed in osmium vapour fixed in a solution containing equal parts of 2 per cent (w/v) osmium tetroxide and saturated mercuric chloride solutions. It is apparent that the Parducz's fixative was far better for this species than were the methods of Curds *et al.* (1974),whereas the reverse was true for the species *Euplotes rariseta* Curds, West & Dorahy, 1974. These results suggest therefore that the choice of fixative may vary with the species under consideration.

RESULTS

Euplotes moebiusi Kahl, 1932

DIAGNOSIS. Medium (60 μm long, 40 μm wide), ovoid freshwater hypotrich with 10 frontoventral, 5 transverse and 4 caudal cirri. Ventral surface heavily sculptured with 7 ridges, dorsal surface with 5 longitudinal ridges. Adoral zone with 35–40 membranelles which extend two-thirds the length of the cell. Dorsal silver-line system with 5 longitudinal rows of narrow polygons interspersed with an irregular network of larger polygons ; 7 dorsolateral kineties bearing a maximum of 11 dorsal cilia. Macronucleus **3**-shaped, micronucleus small, situated anteriorly.

Slides showing silver-line systems, ventral ridges and nuclei have been deposited in the slide collection of the B.M. (N.H.), Reg. Nos. 1973:4:14:1–5.

DETAILED DESCRIPTION. It can be seen from the size distribution data given on Fig. 1 that *Euplotes moebiusi* is a medium-sized species and is 62·25 ± 6·6 μm long and 39·45 ± 5·87 μm wide. The outline shape of the body is oval and there is a definite notch at the anterior end of the body where the adoral zone of membranelles (AZM) begins. The ventral surface is heavily sculptured with 7 ridges. (Fig. 2). One flattened ridge runs along the edge of the peristome and terminates posteriorly in a sharp point. One short ridge is restricted to the anterior half of the body and lies between the front-ventral cirri separating cirrus streak I and II from streak III (using the method of cirrus numeration of Wallengren, 1900). Three short ridges are confined to the posterior and lie between the transverse cirri. One ridge stretches the entire length of the body beginning at the anterior notch (between streaks III and IV) and terminating between the transverse cirri III 1 and IV 1. One medium length ridge is restricted to the central portion of the body and separates cirri V 3 and VI 2 from cirrus V 2. The positions and shapes of these ridges are similar to those figured by Kahl (1932). There are 5 longitudinal ridges on the dorsal surface.

Euplotes moebiusi has 10 frontoventral cirri which are distributed as shown in Figs. 2 and 3b. The arrangement resembles that of *E. charon*. There are 5 transverse and 4 caudal cirri. No specimens were observed with 3 caudal cirri as was shown in the original descriptions by Kahl (1932). The AZM is composed of 35–40 membranelles and its extends two-thirds of the way down the body (Fig. 2).

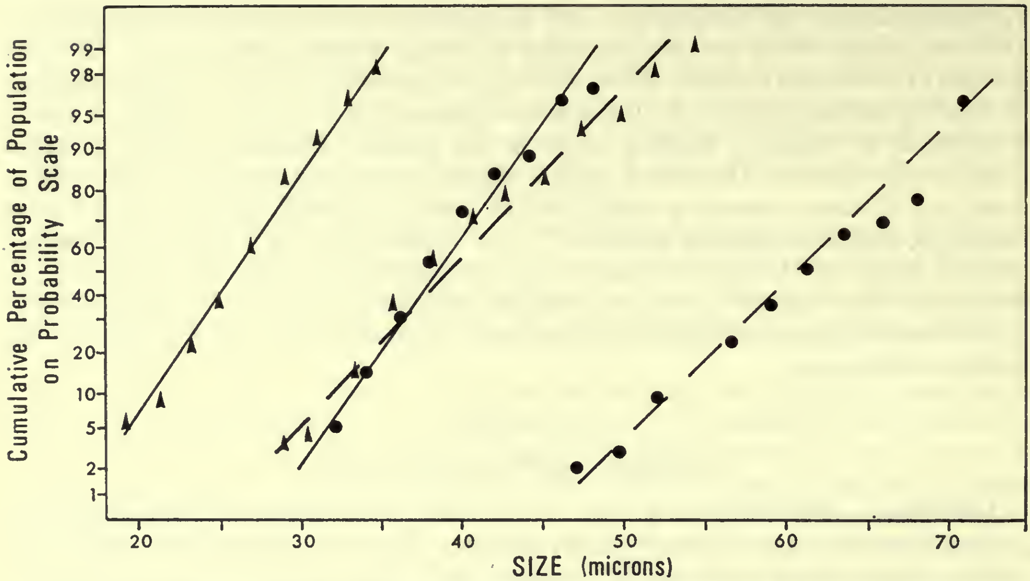

FIG. 1. Size distribution data of *Euplotes moebiusi* (broken lines) and *Euplotes affinis* (continuous lines). Triangles denote width of cells, circles denote length.

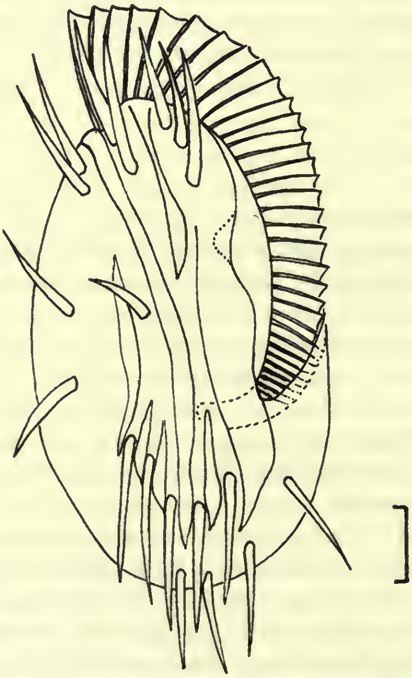

FIG. 2. Ventral aspect of *Euplotes moebiusi* showing cirri and ridges (scale represents 10 μm).

The geometry of the dorsal silver-line system of *Euplotes moebiusi* differs from any of those published. It consists (Fig. 3a) of 5 ladder-like longitudinal rows of narrow polygons with the pits of the dorsal cilia or bristles positioned on the right. In other *Euplotes* spp. with a double *patella*-type of dorsal argyrome the dorsal pits are situated on the left of the rows of smaller polygons. In addition, an irregular network of polygons, resembling that of *E. mutabilis* Tuffrau, 1960, is sandwiched between the ladder-like rows. There are 7 dorsolateral kineties with the central kineties bearing a maximum of 11 dorsal bristles. The ventral silver-line network (Fig. 3b) is a conventional series of irregular polygons whose general pattern closely resembles that of *E. patella* Muller, 1773 (see Tuffrau, 1960).

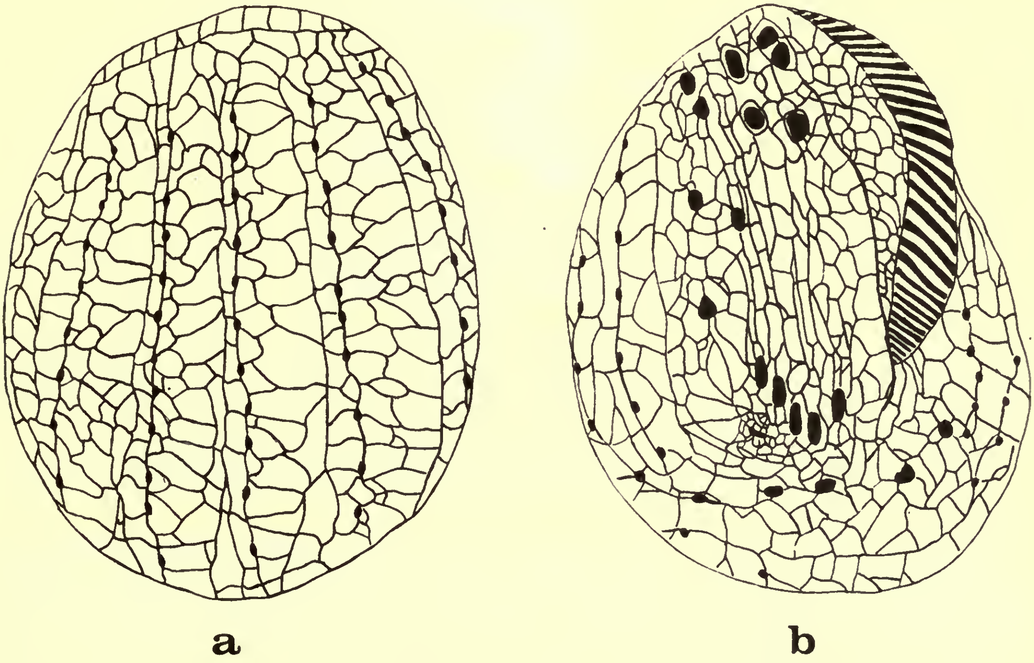

FIG. 3. Silver-line system of *Euplotes moebiusi*, (a) dorsal surface, (b) ventral surface.

The macronucleus of *Euplotes moebiusi* is an irregular **3**-shape (Fig. 4) resembling that of *E. plumipes* Stokes, 1884 (see Tuffrau, 1960), except that the posterior tail is shorter than in that species. The micronucleus is small and lies very close to, and sometimes overlaps, the left anterior edge of the macronucleus.

Euplotes affinis Dujardin, 1842

DIAGNOSIS. Small (38 μm long, 26 μm wide), ovoid freshwater hypotrich with 9 frontoventral, 5 transverse and 3 caudal cirri. Ventral surface sculptured with 3 prominent ridges and dorsal surface with 5 longitudinal ridges. AZM with 18–20

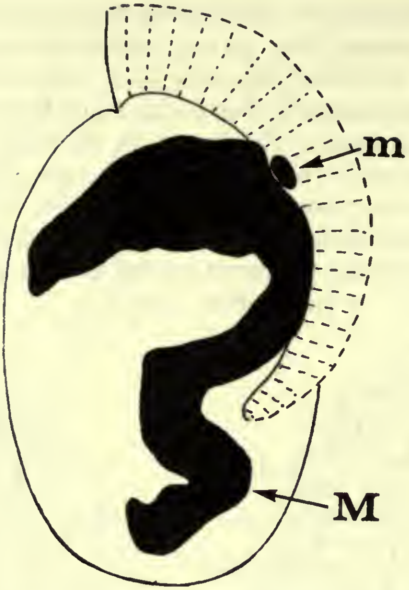

FIG. 4. Ventral view of the nuclei of *Euplotes moebiusi* from a stained preparation (M = macronucleus, m = micronucleus).

membranelles which extends two-thirds the length of the cell. There is a small undulating membrane. Dorsal silver-line system of the double *eurystomus* type with 7 dorsolateral kineties and a maximum of 9 dorsal cilia in the central kineties. The macronucleus is **3**-shaped and there is a small anterior micronucleus.

Slides showing silver-line systems and nuclei have been deposited in the slide collection of the B.M. (N.H.), Reg. Nos. 1973:9:26:1–10.

DETAILED DESCRIPTION. *Euplotes affinis* is one of the smaller freshwater species whose dimensions are 38·4 ± 4·3 μm long and 25·8 ± 4·0 μm wide. The size distribution data of this species are compared with those of *E. moebiusi* in Fig. 1. The outline shape of *E. affinis* resembles that of *E. moebiusi* and there is a marked notch at the anterior of the cell which denotes the origin of the AZM. The ventral surface is heavily sculptured by 3 longitudinal ridges (Fig. 5) which travel almost the entire length of the cell. The outer pair of ventral ridges flank the transverse cirri at the posterior end of the body and terminate anteriorly between cirrus streaks I and II and between streaks V and VI. There are 3 other minor ridges that are restricted to the posterior end of the cell and these lie between the transverse cirri. The positions and shapes of the complete ventral ridging conforms closely with those figured by Kahl (1932). The dorsal surface is also heavily sculptured with 5 longitudinal ridges.

Euplotes affinis has 9 frontoventral cirri whose distribution is shown in Figs. 5 and 6b. There are 5 transverse cirri and 3 caudal cirri ; one of the caudals is larger than the others and is held out stiffly to the right in a manner similar to that of *E. rariseta* (see Curds *et al.* 1974). No specimens have been observed with 4 caudal cirri as was shown in the original descriptions of *E. affinis* by Dujardin (1841), although Kahl (1932) described the variety *E. affinis* forma *tricirratus* which had 3 caudal cirri. The AZM of *E. affinis* extends two-thirds the length of the body and is composed of 18–20 membranelles which is approximately half the number found in *E. moebiusi.*

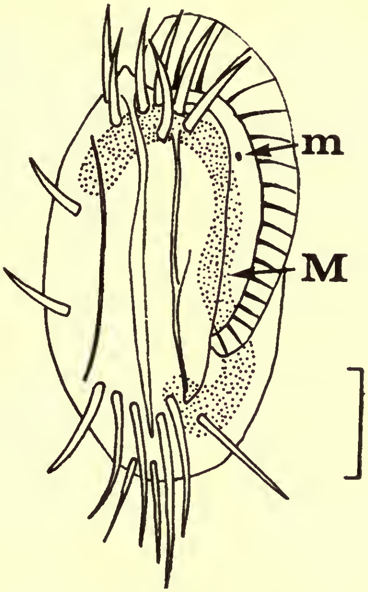

Fig. 5. Ventral aspect of *Euplotes affinis* showing cirri, ridges and nuclei (scale represents 10 μm, M = macronucleus, m = micronucleus).

The dorsal and ventral silver-line systems are shown in Fig. 6. The geometry of the dorsal argyrome (Fig. 6a) is of the double type resembling that of *Euplotes eurystomus* Wrzesniowski, 1870. There are 7 dorsolateral kineties in *E. affinis* and the central kineties bear a maximum of 9 dorsal cilia. The ventral silver-line system is of a common type consisting of a series of relatively few polygons.

The macronucleus is **3**-shaped and resembles those of *Euplotes harpa* Stein, 1859 and *E. plumipes* (see Tuffrau, 1960). The micronucleus is small and is situated at the anterior edge of the macronucleus.

Euplotes parkei sp. n.

Diagnosis. Small (41 μm long, 30 μm wide) euryhaline species ; broadly oval in outline. Dorsal surface with 6 low longitudinal ridges and ventral surface with 7 minor ridges. AZM approximately two-thirds body length, composed of 18 membranelles. A deep pocket near the cytostome bears an undulating membrane. Usually 8, but rarely 9, frontoventral cirri ; 5 transverse and 4 caudal cirri. There are 8 dorsolateral kineties with a maximum of 11 dorsal cilia in the central kineties.

Dorsal silver-line system of the double *eurystomus*-type. Macronucleus C-shaped with anteriorly situated micronucleus.

Type slides showing silver-line systems and nuclei have been deposited in the slide collection of the B.M. (N.H.). Holotype Reg. No. 1973:4:2:1, and paratype Reg. Nos. 1973:4:2:2–5.

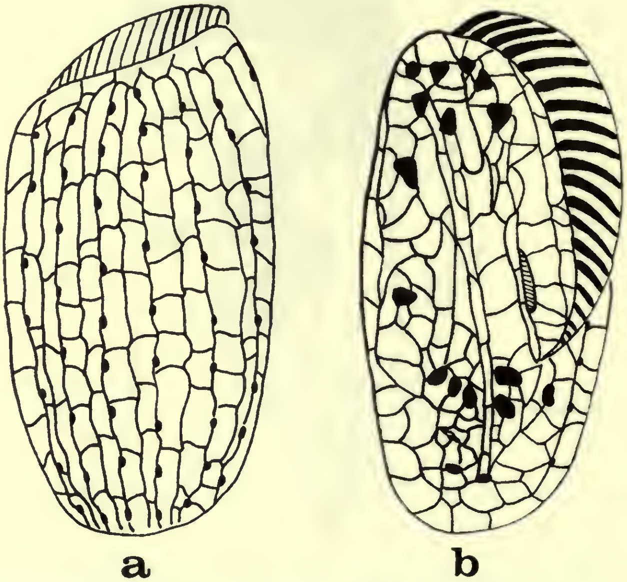

Fig. 6. Silver-line system of *Euplotes affinis*, (a) dorsal surface, (b) ventral surface.

Detailed description. This is a small euryhaline species (41·2 ± 5·6 μm long, 30·6 ± 5·3 μm wide) whose size distribution data are given in Fig. 7. It is broadly oval in outline shape with the dorsal surface sculptured with 6 relatively low longitudinal ridges. To the left of each ridge is a parallel row of pits from which the short (2 μm) dorsal bristles emerge (Pl. 1, figs. c & d). The ventral surface also bears 7 longitudinal ridges (Pl. 1, fig. a) but these are not as prominent as in *Euplotes moebiusi*. One ventral ridge travels the complete length of the body along the extreme edge of the peristome, while the other 6 are relatively short and are confined to the posterior half of the cell. The transverse cirri arise from between these 6 minor ridges. The AZM extends two-thirds the length of the body and is composed of 18 membranelles. There is an undulating membrane situated in a deep pocket on the right of the peristome in the proximity of the cytostome.

This species of *Euplotes* usually bears 8 frontoventral cirri which are arranged as shown in Figs. 8, 9b and Pl. 1, fig. a ; however, a 9th frontoventral cirrus is occasionally present within the same clone and this lies in a position V 2 (Pl. 1, fig. b). The 9th frontoventral cirrus has been found only in animals cultured in freshwater Erdschreiber solution even though the marine cultures have been searched thoroughly

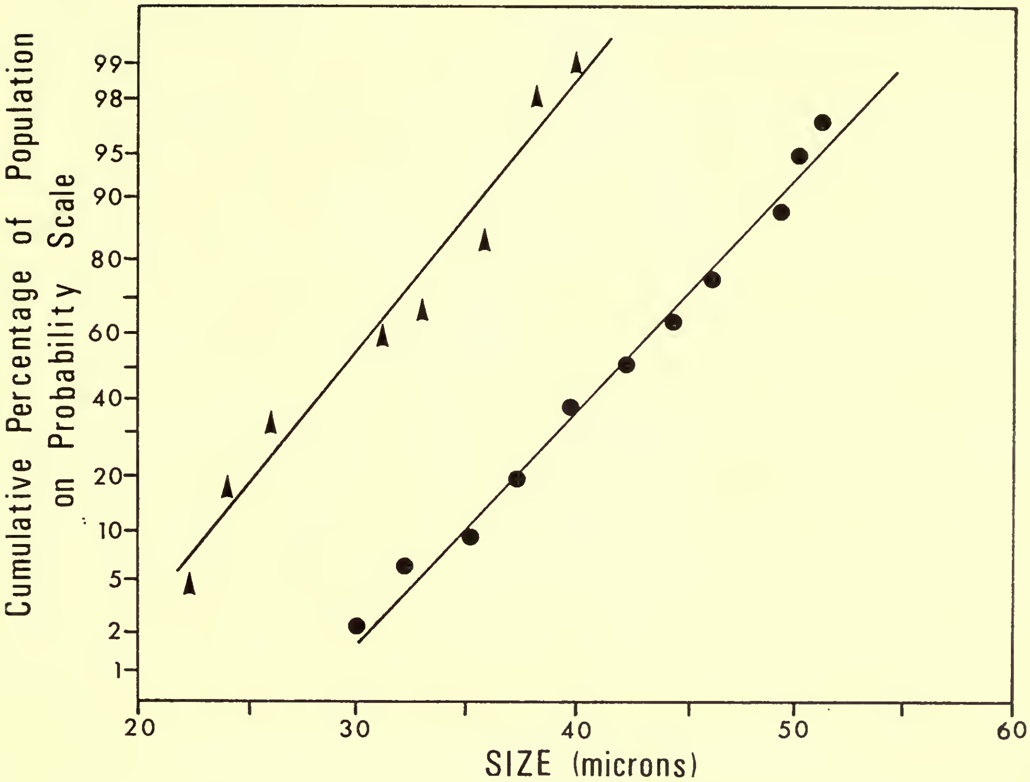

FIG. 7. Size distribution data of *Euplotes parkei*. Triangles denote width and circles length of the cells.

for this variant. It is not yet known if the salinity of the culture plays any part in promoting this type of intraspecific polymorphism. The 5 long transverse and 4 caudal cirri were constant in their numbers.

There are 8 dorsolateral kineties in this species and the central kineties bear a maximum of 11 dorsal cilia. The dorsal and ventral silver-line systems are shown in Fig. 9. The disposition of the dorsal argyrome (Fig. 9a) is of the double type resembling that of *Euplotes eurystomus*. The ventral silver-line system consists of a series of few but large polygons and in this respect resembles that of *E. cristatus* Kahl, 1932 (see Tuffrau, 1960). The dorsal argyrome can be seen on some scanning-electron micrographs (Pl. 1, figs. c & d) as a series of tiny specks. The macronucleus (Fig. 8) is C-shaped and the micronucleus is situated close to the left anterior edge of the macronucleus.

DISCUSSION AND CONCLUSIONS

Euplotes moebiusi is one of the nine species of the genus whose silver-line system had not been fully described, and its identity relied solely upon the brief description of Kahl (1932). It is evident from the description of the silver-line system given in

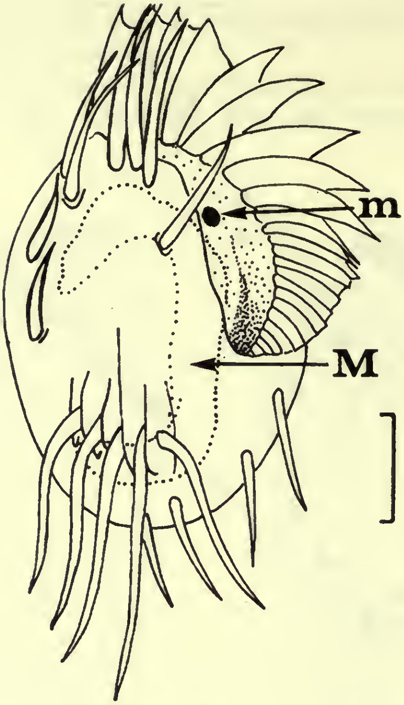

FIG. 8. Ventral aspect of *Euplotes parkei* showing cirri, ridges and nuclei (scale represents 10 µm, M = macronucleus, m = micronucleus).

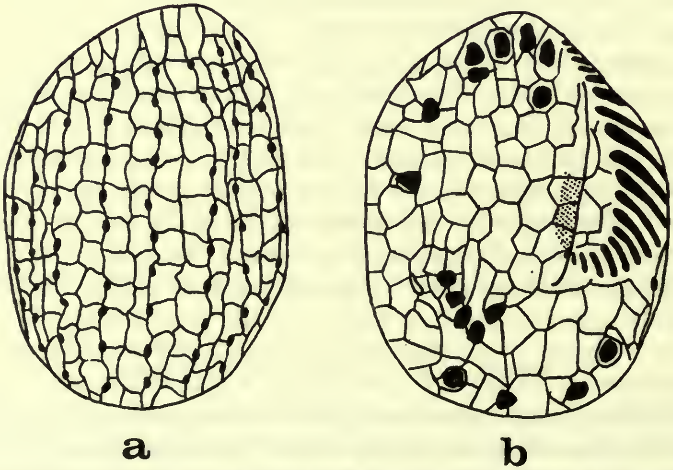

FIG. 9. Silver-line system of *Euplotes parkei*, (a) dorsal surface, (b) ventral surface.

the present paper that *E. moebiusi* is a distinct species and is not a synonym of *E. charon* as was suggested by Tuffrau (1960).

Before the completion of the present studies it was the opinion of the author that *Euplotes moebiusi* was likely to be a synonym of *E. affinis* because of the similarities between the two species which may be listed thus ; they both have the same general shape and size with a definite anterior notch ; both have ventral ridges of similar appearance ; both *E. moebiusi* and *E. affinis* are reported to have 4 and 3 caudal cirri variants called *E. moebiusi* forma *quadricirratus* and *E. affinis* forma *tricirratus* respectively ; both have **3**-shaped macronuclei and both may be found in organically polluted freshwater habitats. This meant that there was only one known character left to separate the two species, namely the presence or absence of frontoventral cirrus V 2. In view of the findings presented in this paper concerning the intraspecific polymorphism of *E. parkei* due to the variability of cirrus V 2 it is evident that the presence or absence of this cirrus is not as reliable a character as was originally believed. The results presented here however have clarified the situation considerably and *E. affinis* can now be distinguished from *E. moebiusi* by the 5 characters listed in Table 1. The most reliable character is the geometry of the dorsal silver-line system which is completely different in the two species (compare Figs. 3b & 6b). In the author's opinion *E. affinis* should not be regarded as a synonym of *E. charon* as was suggested by Tuffrau (1960), and there are sufficient reliable characters to regard *E. affinis* as a species distinct from all others.

TABLE 1

List of characters which serve to distinguish between *Euplotes moebiusi* and *Euplotes affinis*

Character	*E. moebiusi*	*E. affinis*
Number of frontoventral cirri	10	9
Number of membranelles in AZM	35–40	18–20
Maximum number of dorsal cilia in mid-dorsolateral kineties	11	9
Dorsal argyrome	Complex	Double *eurystomus*
Ventral argyrome	Many small polygons	Few large polygons

Agamaliev (1967) reported intraspecific polymorphism in the number of frontoventral cirri in his description of *Euplotes raikovi* Agamaliev, 1966. In the Caspian Sea strain of *E. raikovi*, Agamaliev (1967) noted that there were 7 or 8 frontoventral cirri and indicated that cirrus V 2 was that which did not develop in some specimens. However in a recent paper, Washburn & Borror (1972) described a strain of *E. raikovi*, isolated from a sand sample taken from the New Hampshire coast of the U.S.A., in which they could not find an 8th cirrus (cirrus V 2) although they did observe a completely barren plaque in each case. Negative evidence such as this can never be conclusive and one must accept that Agamaliev's strain did exhibit polymorphism of cirrus V 2 as he claimed, particularly in the light of the photographic evidence presented in this paper where there can be no doubt that *E. parkei* may have 8 or 9 completely normal frontoventral cirri. More work must be carried out on the morphogenesis of *E. parkei* particularly on the fate of cirrus V 2, but the evidence so far obtained indicates that there is not even a barren plaque in the case of *E. parkei* specimens with 8 frontoventral cirri. Furthermore, more work is needed to test adequately whether or not intraspecific polymorphism such as this can be induced by adjusting the salinity of the culture medium or if the results so far obtained can be attributed to pure chance.

It is possible that one of the reasons why *Euplotes parkei* has remained unnoticed until now is because none of its characters, in isolation, will distinguish this species from all others. A combination of characters is required to do so, but there can be little doubt that this small euryhaline *Euplotes* is a separate and distinct species. The following species have the combination of characters – a double dorsal argyrome with 8 or 9 frontoventral, 5 transverse and 4 caudal cirri – *E. aediculatus* Pierson, 1943 ; *E. amieti* Dragesco, 1970 ; *E. aspheronicus* Agamaliev, 1966 ; *E. diadaleos* Diller & Kounaris, 1966 ; *E. eurystomus* ; *E. octocarinatus* Carter, 1972 ; *E. patella* ; *E. patella* forma *latus* Agamaliev, 1967 ; *E. plumipes* ; *E. tegulatus* Tuffrau, 1960 ; *E. tuffraui* Berger, 1965 ; *E. variabilis* Stokes, 1887 (see Carter, 1972) ; and *E. zenkewitchi* Burkovsky, 1970. However only four of these, *E. aediculatus*, *E. eurystomus*, *E. variabilis* and *E. octocarinatus*, have 8 dorsolateral kineties. Since *E. octocarinatus* has a *patella*-like double dorsal argyrome there are only three remaining species with which to compare and contrast *E. parkei.* All three of these *Euplotes* spp. are large (over 100 μm long) and have at least 40 membranelles in the AZM, whereas *E. parkei* is small (under 50 μm long) and has less than 20 membranelles. Furthermore, the shapes of the macronuclei differ and all three species have many more dorsal cilia than *E. parkei.*

It is evident therefore that *Euplotes parkei* differs from all previously described species of *Euplotes* and the differences are considered to be sufficiently distinct for this organism to be designated as a separate species. It is named *Euplotes parkei* after Dr Mary Parke of the Marine Biological Station Plymouth who first isolated and cultivated this hypotrich. Following the revised classification of the Committee on Taxonomic Problems of the Society of Protozoology (Honigberg *et al.*, 1964), *Euplotes parkei* is placed into class Ciliatea Perty, 1852, order Hypotrichida Stein, 1859, family Euplotidae Ehrenberg, 1838.

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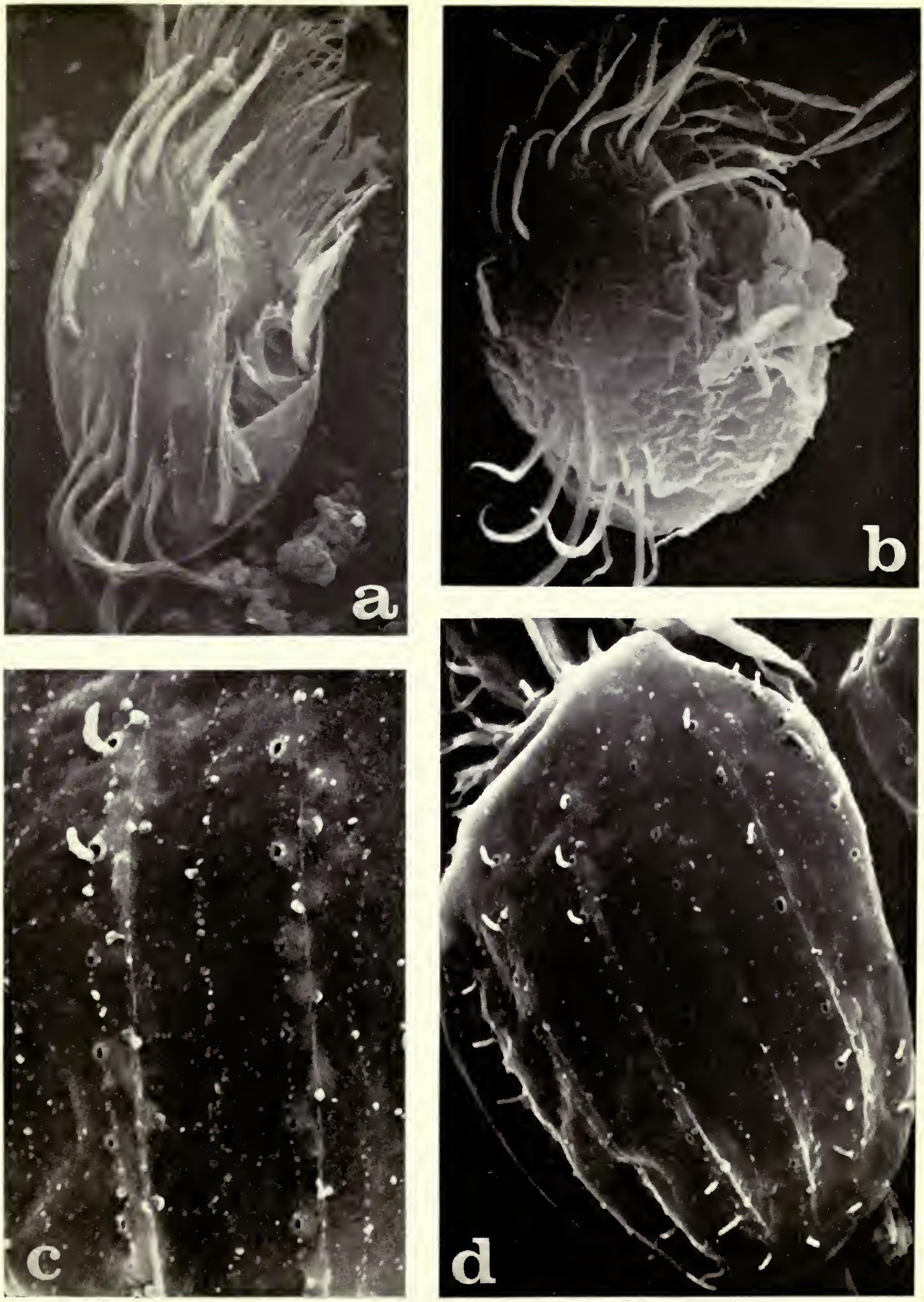
PLATE 1

Scanning-electron micrographs of *Euplotes parkei*

a. Ventral view showing ridges and cirri. Cell fixed in Parducz's (1967) fixative.
b. Ventral view of a 9 frontoventral cirri variant. Cell killed and fixed following the methods of Curds *et al.* (1974).
c. Dorsal view showing the outline of the dorsal argyrome as specks.
d. Dorsal view showing ridges, dorsal cilia and outline of argyrome.


a
b
c
d

NEW RECORDS OF BATS FROM SOUTH-EASTERN ASIA, WITH TAXONOMIC NOTES

By J. E. HILL

INTRODUCTION

BATS from Malaya, Java and Sulawesi (Celebes) identified in recent years at the British Museum (Natural History) have included specimens representing a number of poorly known species and thereby of taxonomic interest and importance, or which provide further distributional records. The majority of the Malayan specimens have come to London through the agency of Lord Medway and were collected by him or by Mr G. C. Yong. A further interesting specimen from Malaya has been provided by Dr D. R. Wells of the School of Biological Sciences, the University of Malaya. The Indonesian specimens are from a collection submitted for identification by Captain P. F. D. Van Peenen, M.C., U.S.N., Officer in Charge, U.S. Naval Medical Research Unit No. 2, Djakarta Detachment. My thanks are due also to Dr G. G. Musser and Dr Karl F. Koopman of the American Museum of Natural History, New York, who waived a prior claim to the Sulawesian specimens, and to Dr H. W. Setzer of the United States National Museum of Natural History, the Smithsonian Institution, Washington, who arranged the loan of one of the specimens discussed. Measurements are in millimetres : unless otherwise indicated, the specimens have been donated to the collections of the British Museum (Natural History).

SYSTEMATIC SECTION

Chironax (?) melanocephalus (Temminck, 1825)

Sulawesi : Soroako, south Sulawesi. ♀ (young adult) B.M. 73.1802.

Chironax has been unreported hitherto from Sulawesi. This young adult specimen differs in a number of features from Malayan material referred to *C. melanocephalus* and apparently also in some ways from Javan specimens, of which none is available for comparison. Consequently, it is referred to *C. melanocephalus* with considerable hesitation.

This Sulawesian specimen lacks the distinctive blackish cap usually characteristic of *Chironax* although the nape and crown are darker brown than the back which is warm brown, tinged with grey over the shoulders. The throat and the sides of the neck are creamy white, the belly yellowish white and the flanks brown, this colour extending across the hinder part of the ventrum. In colour the specimen agrees quite well with the original description by Temminck (1825 : 190) of specimens from

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Java : it differs from mainland specimens in its generally paler dorsal surface and also lacks any rufous or orange at the sides of the neck, a feature sometimes found in mainland examples.

There are some differences in wing structure when a comparison is made with mainland and Javan specimens. In particular, the fifth metacarpal is relatively a little longer, and the second phalanges of the third, fourth and fifth digits are relatively a little shorter, those of the fourth and fifth digits not exceeding in length the first phalanges of their respective digits as they do in continental and Javan examples. The relevant wing structures are summarized in Table 1 and in these respects it can be seen that the Sulawesian specimen approaches the closely related genus *Balionycteris*.

Table 1

Wing indices of *Chironax* and *Balionycteris*
Length of forearm = 1000

	Chironax			*Balionycteris*
	Malaya	Java*	Sulawesi	
Third digit				
Metacarpal	677–711	640 635	705	710–780
First phalange	474–533	489 488	507	474–548
Second phalange	584–657	640 623	568	559–653
Fourth digit				
Metacarpal	617–679	617 578	641	693–739
First phalange	368–415	373 378	373	374–430
Second phalange	396–444	418 422	360	352–415
Fifth digit				
Metacarpal	659–704	640 622	708	712–764
First phalange	318–360	344 322	319	330–364
Second phalange	339–384	348 344	317	312–354

* 'Co-types' of *C. melanocephalus*, from Andersen (1912 : 676).

Cranially the specimen from Sulawesi is a little smaller than the mainland examples but its cranial dimensions fall within the range of variation reported for the Javan 'cotypes' by Andersen (1912 : 678). The supraorbital region is a little more swollen medianly than in continental specimens and the postorbital processes are more massively developed. As might be expected in a young adult, the premaxillae are not solidly fused anteriorly. The post-canine teeth are generally rather smaller than are those of specimens from the mainland, with pm^4 more rounded, less rectangular in outline, while pm^3 lacks completely the antero-external cusp customary in *C. melanocephalus*. This cusp, however, is very small in some Malayan specimens.

Chironax melanocephalus has been reported from Java, Sumatra (Chasen, 1940 : 28, 30), Nias Island (Thomas, 1923 : 252), Malaya (Chasen, loc. cit. ; Hill, 1961 : 640) and from southern Thailand (Hill and Thonglongya, 1972 : 181), who also reported further Malayan specimens. The presence of *Chironax* in Sulawesi is not unexpected but the exact taxonomic status of the Sulawesian population must remain to some extent uncertain until further specimens from Sulawesi and Java are available.

Measurements of the specimen from Sulawesi : length of forearm 44·2 ; length of third metacarpal 31·1 ; length of its first phalange 22·4 ; length of its second phalange 25·1 ; length of fourth metacarpal 28·3 ; length of its first phalange 16·5 ; length of its second phalange 15·9 ; length of fifth metacarpal 31·3 ; length of its first phalange 14·1 : length of its second phalange 14·0 ; greatest length of skull 22·2 ; condylobasal length 21·4 ; condylocanine length 20·8 ; palatal length 11·1 ; palation to incisive foramina 9·3 ; palation to basion 8·2 ; length orbit–nares 5·2 ; width of braincase 9·8 ; mastoid width 10·0 ; zygomatic width 14·3 ; m^1–m^1 (crowns) 6·3 ; p^4–p^4 (crowns) 6·3 ; lachrymal width 6·1 ; c^1–c^1 (cingula) 4·3, (alveoli) 4·0 ; postorbital width 5·5 ; interorbital width 4·9 ; width of mesopterygoid fossa 2·9 ; width between p^4–p^4 3·8 ; width between bases of canines 1·9 ; orbital diameter 5·6 ; length of mandible from condyle 16·0 ; length of complete mandible from both condyles 15·2 ; coronoid height 7·3 ; c–m^1 (crowns) 6·9 ; c–m_2 (crowns) 7·5 (in order of Andersen, 1912 : 678, with interpolations).

Measurements of teeth : length × width of pm^3 1·7 × 1·1 ; of pm^4 1·7 × 1·2 ; of m^1 1·3 × 0·9 : of pm_1 0·7 × 0·7 ; of pm_3 1·6 × 1·1 ; of pm_4 1·7 × 1·2 ; of m_1 1·4 × 0·9 ; of m_2 0·8 × 0·6 (notation of teeth based on Andersen, 1912 : 680).

It may be noted that by error the illustration of *Chironax* in the editions and printings of Walker (1964, 1965, 1968) is not of *C. melanocephalus* but of a young *Rousettus*.

Rhinolophus pusillus Temminck, 1834

Malaya : Pasang Kamunting, Kg. Ginting, Penang. ♀ B.M. 73.608.

Andersen (1905 : 121) summarized the many different forms of *Rhinolophus* before then confused under *Rhinolophus minor* Horsfield, 1824, envisaging a *lepidus* group composed of *lepidus*, *minor* and *subbadius* subgroupings. Later, the same author (1918 : 376) in a paper issued on his behalf by Oldfield Thomas renamed this the *pusillus* group and added a number of briefly diagnosed new forms. Tate and Archbold (1939 : 3) listed the names allocated to the group, retaining the subdivisions proposed by Andersen. These authors included *R. minor* and *R. pusillus* as distinct species but Andersen (1905 : 126) considered *pusillus* a synonym of *minor* : however, *Rhinolophus minor* Horsfield, 1824 is preoccupied (Chasen, 1940 : 38 ; Ellerman & Morrison-Scott, 1951 : 116).

The species has not hitherto been recorded from the Malay Peninsula : this specimen from Penang agrees closely with a small series from Java and with one specimen from Madura identified by Andersen as *R. pusillus*, the species that he called *R. minor* in his early investigation (1905 : 121) of the group. There is close agreement also between the Penang specimen and a series in the collections of the British Museum (Natural History) from the island of Tioman, off the east coast of Malaya. *Rhinolophus pusillus* is small, easily recognized by its upright triangular connecting process and small skull (Table 2).

TABLE 2

Measurements of *Rhinolophus pusillus*

Registration No.	Sex	Length of forearm	Greatest length of skull to canine	Condylocanine length	Width across rostral swellings	Least interorbital width	Zygomatic width	Width of braincase	Mastoid width	c^1–c^1	m^3–m^3	c–m^3	Length of complete mandible	c–m_3	Locality
9.1.5.176	♀	39·9	15·2	–	4·5	2·2	–	–	–	4·2	–	–	10·1	–	Java
9.1.5.177	♀	37·8	–	–	4·3	2·1	7·8	–	–	3·8	5·7	5·7	–	6·0	Java
9.1.5.178	♀	39·4	–	–	4·3	–	–	–	–	–	5·9	5·8	10·4	6·3	Java
61.1747	♀	39·3	15·6	13·6	4·1	2·1	7·8	7·1	7·8	3·8	5·5	5·6	9·9	5·9	Java
10.4.7.8	♂	–	15·7	13·7	4·3	2·0	7·5	6·8	7·7	3·8	5·6	5·8	10·1	6·2	Madura
61.1679	♂	38·0													Tioman I.
61.1682	♀	38·1	15·7	13·6	4·2	2·0	8·1	6·8	7·7	3·8	5·7	5·8	10·5	6·2	Tioman I.
61.1684	♀	39·7													Tioman I.
1973.608	♀	39·3	15·8	13·7	4·3	2·2	8·2	6·9	7·8	3·9	5·8	5·6	9·9	6·0	Penang
28.7.1.18	–	37·3	15·3	–	4·4	2·0	8·0	–	–	3·8	5·8	5·8	9·9	6·3	South Vietnam
28.7.1.19	♂	37·9	15·6	13·8	4·3	2·0	8·2	6·8	7·7	3·8	5·9	5·9	10·0	6·4	South Vietnam

Andersen (1905 : 126) recorded *R. minor* (= *pusillus*) from Darjeeling, Thailand and Java. As Osgood (1932 : 215) pointed out, when Andersen wrote further on the *pusillus* group (1918 : 376) and named *R. blythi blythi* and *R. b. szechwanus*, evidently he had concluded that the mainland forms were separable from *pusillus* of Java. Indeed, Andersen has re-labelled the specimens in the British Museum (Natural History) on which the continental records of *pusillus* were based as '*szechwanus*'. Osgood considered that specimens obtained in Cochin China (South Vietnam) by Delacour and Lowe (B.M. 28.7.1.18–19) and referred to *pusillus* by Thomas were doubtless closely related if not identical to *R. blythi calidus* Allen, 1923, to which Osgood referred a specimen from Tonkin (North Vietnam), suggesting that since the distinctions between the various forms seemed unclear it might be preferable to treat them as races of *pusillus*, the earliest name. There is every probability, therefore, that *Rhinolophus pusillus* Temminck, 1834 must replace *R. blythi* Andersen, 1918 if this is thought to be specifically distinct. Ellerman and Morrison-Scott (1951 : 117) considered *R. blythi* a subspecies of *R. cornutus* Temminck, 1835, to which Van Peenen, Ryan & Light (1969 : 61) allocated specimens from South and North Vietnam (presumably those reported by Osgood) and from Thailand. However, Wang *et al.* (1962 : 556, 558, 568) reported *R. cornutus pumilus* Andersen, 1905 and *R. blythi* (as a species) from Kwangsi.

Rhinolophus acuminatus acuminatus Peters, 1871

Malaya : Kuala Kenarong, Ulu Perak. ♂, ♀ B.M. 73.609–610.

Rhinolophus acuminatus has remained unreported from Malaya although there is a number of records from Thailand, Laos and Cambodia (Hill & Thonglongya, 1972 : 185), and the species occurs also on Sumatra and the nearby islands of Engano and Nias, on Borneo, Java and on Lombok. Like those from Thailand and Laos previously reported, these Malayan specimens agree closely in size with *R. a. acuminatus* from Java. Both have been preserved in alcohol. The female is very similar in colour to reddish brown examples from Java, its dorsal surface brown, tinged with russet, especially posteriorly. Ventrally it is greyish brown, the hairs pale based, pale grey brown for much of their length and extensively tipped with grey. Dorsally, the male is browner, lacking russet, lightly tipped over the shoulders with silver grey : ventrally it is paler than the female, more nearly fawn, with a brownish tinge.

Measurements (♂ B.M. 73.609, ♀ B.M. 73.610) : length of forearm 49·1, 47·8 ; width of noseleaf 8·1, 8·0 ; greatest length of skull to canine 21·5, 20·5 ; condylo-canine length 19·2, 18·2 ; width across nasal swellings 6·1, 5·8 ; least interorbital width 2·5, 2·7 ; zygomatic width 11·6, 11·3 ; width of braincase 9·0, 9·0 ; mastoid width 10·2, 9·9 ; c^1–c^1 5·6, 6·0 ; m^3–m^3 8·3, 8·3 ; c–m^3 8·6, 8·0 ; length of complete mandible 15·2, 13·7 ; c–m_3 9·2, 8·8.

The subspecies of *R. acuminatus* as they are defined by Andersen (1905 : 132, 1906 : 657) seem separable only by relatively small features. Mainland specimens have the lower part of the lateral margins of the sella more or less parallel as in *acuminatus* from Java and in *audax* from Lombok, the sella not abruptly widened basally as in *sumatranus* from Sumatra or *circe* from Nias, or in *calypso* from Engano in which the sella, although widened, is less so than in these but which has a very wide noseleaf. There seem no consistent size differences between the subspecies : a series from Java suggests a degree of sexual dimorphism in size, with females tending to be a little smaller than males.

Myotis horsfieldii horsfieldii (Temminck, 1840)

Sulawesi : Wawondula, south Sulawesi. ♀ B.M. 73.1804.

This is the first of *Myotis horsfieldii* to be reported from Sulawesi, the species being known otherwise from Java, Borneo (Medway, 1965 : 60), Malaya and perhaps Thailand (Hill, 1972 : 31). For the present it is referred to the nominate subspecies : cranially it corresponds to or slightly exceeds the upper limits of size for Javan specimens as represented in London, but these derive from a single series from one locality. It is similar in size to the larger of Bornean specimens (*M. h. lepidus* (Thomas, 1915)) but no more than three examples of this subspecies are available. Medway (1965 : 60) suggests that *lepidus* from Borneo may be distinguished from Javan *horsfieldii* by slightly shorter skull and slightly narrower braincase, conditions not supported by the available specimens. The condylobasal length of eighteen Javan specimens ranges from 13·2 to 14·7, in three from Malaya from 13·7 to 14·3 and from 14·3 to 14·7 in three from Borneo : the width of the braincase varies from 6·9 to 7·4 in Javan examples, from 6·9 to 7·3 in those from Malaya and from 7·1 to 7·3 in the specimens from Borneo, which include the holotype of *lepidus*. The Bornean subspecies appears therefore to be only weakly if at all separable.

Measurements of the specimen from Sulawesi : length of forearm 37·7 ; greatest length of skull 15·7 ; condylobasal length 14·4 ; condylocanine length 13·8 ; least interorbital width 3·6 ; zygomatic width — ; width of braincase 7·4 ; mastoid width 8·0 ; c^1–c^1 4·2 ; m^3–m^3 6·0 ; c–m^3 5·7 ; length of complete mandible 11·3 ; c–m_3 6·2. The registration numbers of Malayan specimens measured by Hill (1972 : 31) are incorrectly assigned. The measurements cited are of B.M. 61.2133 (forearm only), B.M. 65.320, B.M. 65.321, and of ♀ B.M. 16.4.21.16 (this number omitted) from Batu Burong, Pahang, in that order.

Pipistrellus circumdatus (Temminck, 1840)

Java : Cibodas (= Tjibodas), Cianjur, west Java, 06°45′ S, 107°00′ E, at 1350 m. ♂. Original number 1435. Bogor Museum No. 10069 (at present at United States National Museum of Natural History, the Smithsonian Institution, Washington).

Kandang Badak, Cianjur, west Java, 06°47′ S, 106°59′ E, at 2425 m. ♂. Original number 1761. U.S. Naval Medical Research Unit No. 2, Djakarta Detachment.

Situ Gunung, Sukabumi (= Soekaeboemi), west Java, 06°50′ S, 107°55′ E, at 1000 m. ♀. B.M. 73.1805.

Malaya : Telecommunications Tower, Fraser's Hill, Pahang. ♂ B.M. 73.618.

Extant specimens of the poorly known south-east Asian species *Pipistrellus circumdatus* (Temminck, 1840) were briefly reviewed recently by Hill (1972 : 189), who described a closely related species, *P. societatis*, from Malaya. At that time, no more than five examples of *P. circumdatus* were known.

Although Temminck (1840 : 215) remarked that Boie and Macklot, who first obtained the species in the Tapos district of Java, sent several individuals to the Musée des Pays-Bas (the Rijksmuseum van Natuurlijke Historie, Leiden), the catalogues by Jentink (1887 : 277 ; 1888 : 178) of that collection report only a single specimen, in 1887 as 'one of the types of the species' for the skull, and in 1888 as 'type of the species' for the mounted specimen to which the skull belongs. This specimen remains in the Rijksmuseum van Natuurlijke Historie : a second example from Java, now in the collection of the British Museum (Natural History) (B.M. 7.1.1.401) is from the collection of R. F. Tomes, and since this collector obtained specimens from many sources, including the major museums of his day, it is possible that it is one of the original specimens obtained by Boie and Macklot.

Known continental specimens are limited to three. One, (B.M. 61.12.10.1) in the collection of the British Museum (Natural History), is of uncertain provenance. It came from T. C. Jerdon and is said by Blanford (1891 : 312) to have originated from southern India. Another (A.M.N.H. 114850), in the American Museum of Natural History, is from Pyepat, Upper Burma, and has been reported by Anthony (1941 : 81), Tate (1942 : 250) and by Hill (1972 : 36). The third, listed above, from Fraser's Hill, Pahang, Malaya, was briefly reported by Hill (1972 : 36, footnote). It is therefore of particular interest to record three specimens from Java obtained by the United States Medical Research Unit No. 2, Djakarta Detachment, and to present a more detailed account of the newly collected Malayan specimen.

The specimens from Java agree closely with the description by Temminck and with B.M. 7.1.1.401. The males are exactly similar in colour to this example, the blackish brown dorsal pelage finely but profusely tipped with shining orange or bronze, the ventral pelage dark brown, the hairs lightly tipped with grey except on the flanks where the tipping is brownish, sometimes faintly orange. The membranes are black and in B.M. 7.1.1.401 evidently have faded to a browner shade. The female specimen has dorsal pelage a little less finely tipped with orange, the individual orange hair tips slightly more extensive to give a coarser effect : its ventral surface resembles the ventral surface of the other specimens although the tips of the hairs tend to be more yellowish buff, especially anteriorly. Cranially, the specimens conform closely to B.M. 7.1.1.401, described, with the skull of the holotype of *circumdatus*, in the account already published (Hill, 1972 : 36).

The example from Malaya is very similar to the Burmese specimen (A.M.N.H. 114850) discussed by Hill (1972 : 36), its skull differing slightly in a number of features from the skulls of Javan specimens. It is generally a little smaller ; the cranial crests are less prominent, the supraorbital ridges slightly less evident but in this example not terminating in slight tubercles ; the frontal depression is a little shallower but the post-palatal extension is not shorter than in the Javan skulls as is the post-palatal extension of the Burmese example. As in the Burmese specimen, the post-palatal spine is narrow : although broken in two of the Javan skulls examined, in the other two skulls from Javan specimens the spine is more broadly based. There is little difference in the dimensions of the teeth, although the canines of the Malayan specimen are very slightly less massive than are those of the Javan examples.

Initially, a comparison of the Burmese specimen with Javan material suggested (Hill, 1972 : 36) that the mainland and Javan populations might be subspecifically distinct. The new material confirms that small differences exist between the two populations but as yet insufficient specimens are available for any definite conclusion to be drawn. The Malayan specimen is of especial interest since it demonstrates the presence of *P. circumdatus* in Malaya with the newly described *P. societatis*, a closely similar species differing chiefly in smaller size, particularly of the rostrum, palate and dentition, and in its short post-palatal region (length of bony post-palate in four Javan specimens of *circumdatus* 1·5–1·7, in the Malayan specimen 1·7, in the holotype of *societatis* (B.M. 67.1605) 1.1).

Measurements (♂ 1435, ♂ 1761, ♀ B.M. 73.1805 from Java, ♂ B.M. 73.618 from Malaya, in that order) : length of forearm 41·2, 41·1, 42·1, 40·5 ; greatest length of skull 16·0, 16·3, 16·6, 15·5 : condylobasal length 15·7, 15·7, 16·0, 14·9 ; condylo-canine length 15·4, 15·4, 15·7, 14·7 ; palatal length (excluding the post-palatal spine) 8·4, 8·4, 8·6, 8·0 ; length palatal bridge (excluding the post-palatal spine) 6·5, 6·6, 6·8, 6·4 ; length orbit–gnathion 4·2, 4·0, 4·2, 4·1 ; lachrimal width 7·1, 7·2, 7·3, 7·2 ; width across supraorbital tubercles or swellings 6·6, 6·6, 6·7, 6·4 ; zygomatic width 11·4, —, 11·7, — ; least interorbital width 4·2, 4·4, 4·3, 4·3 ; width of braincase 8·0, 8·1, 8·1, 7·9 ; mastoid width 8·7, 8·7, 9·1, 8·5 ; c^1–c^1 5·2, 5·3, 5·4, 5·0 ; m^3–m^3 —, 7·6, 7·7, 7·3 ; c–m^3 6·2, 6·1, 6·3, 5·9 ; length of complete mandible —, 11·9, 11·9, 11·1 ; c–m_3 6·5, 6·4, 6·7, 6·3.

Philetor brachypterus verecundus (Chasen, 1940)

Malaya : Ulu Gombok, Selangor. ♂ B.M. 73.597.

The genus *Philetor* with its sole species *P. brachypterus* is known from New Guinea, Malaya, Sumatra and, doubtfully, from Java and Banka (Hill, 1971 : 140). Its occurrence in Malaya was based initially on two female specimens from Perak originally described as *Eptesicus verecundus* by Chasen (1940 : 53), one the holotype collected on Mount Kledang by Dr R. Hanitsch (now B.M. 47.1437) and the other (at one time in the collections of the former Raffles Museum, Singapore) from an unspecified locality in that State. Medway (1969 : 35) mentions that it has been collected in Selangor. *Eptesicus verecundus* was transferred to *Philetor* by Hill (1966) who considered it a subspecies of *Philetor rohui* Thomas, 1902 from New Guinea : later, the same author (1971) referred *Vespertilio brachypterus* Temminck, 1840 from Sumatra to *Philetor* as a third subspecies, *brachypterus* taking precedence as the specific name.

This further specimen of *P. b. verecundus* has been donated to the collections of the British Museum (Natural History) by Dr D. R. Wells of the School of Biological Sciences, the University of Malaya. Its muzzle, ears and tragus agree closely with those of the holotype : the structure of the penis, hitherto unknown in *verecundus*, is almost exactly like that of *P. b. rohui* (figured by Hill, 1966 : 375, fig. 1), differing only in slightly wider and deeper fissures in the ventral part of the glans.

Cranially there is close agreement with the holotype of *verecundus*. The braincase is very slightly more inflated than in *P. b. rohui* as it is in the holotype : the narial emargination, however, rather wider at the roots of i^{2-2} and broadly V-shaped apically in the holotype of *verecundus*, is in this specimen rather narrower and more rounded at the apex, thus conforming with *rohui* and with the holotype of *P. b. brachypterus* from Sumatra (Hill, 1971 : 141). The upper canines of the specimen from Selangor are a little more massive than in the holotype of *verecundus*, and the Selangor specimen differs from this and from *rohui* in having a narrow rather than wide post-palatal spine, and its basioccipital pits are a little less prominent.

Measurements : length of forearm 35·9 ; greatest length of skull — ; condylobasal length 14·7 ; condylocanine length 14·3 ; lachrimal width 6·7 ; width across anteorbital foramina 5·5 ; least interorbital width 4·6 ; zygomatic width — ; width of braincase 8·3 ; mastoid width 9·0 ; c^1–c^1 5·4 ; m^3–m^3 6·7 ; c–m^3 4·8 ; i^2–m^3 5·6 ; length of complete mandible 10·4 ; c–m_3 4·9.

Miniopterus medius macrocneme Revilliod, 1914

Sulawesi : Wawondula, south Sulawesi. ♀, ♂ B.M. 73.1806–1807.

The length of the forearm and tibia, with the globose, high braincase and slender canines refer these specimens to *M. medius*, hitherto unreported from Sulawesi. They display the less massive dentition characteristic of the easterly subspecies *M. m. macrocneme* which until now has not been known to occur further west than the islands of Ambon and Ceram, in the Molucca Islands.

Measurements (♂ B.M. 73.1807, ♀ B.M. 73.1806) : length of forearm 44·4, 43·3 ; length of tibia 19·1, 18·8 ; greatest length of skull 13·7 ; 13·2 ; condylobasal length 13·1, 12·9 ; condylocanine length 12·6, 12·1 ; least interorbital width 3·4, 3·5 ; zygomatic width 7·4, 7·5 ; width of braincase 7·4, 7·2 ; mastoid width 7·6, 7·5 ; c^1–c^1 3·9, 3·7 ; m^3–m^3 5·4, 5·4 ; c–m^3 5·1, 5·0 ; length of complete mandible 9·7, 9·5 ; c–m_3 5·6, 5·3.

Phoniscus atrox Miller, 1905

Malaya : Tekom Forest Reserve, Jerantut, Pahang. ♂ B.M. 71.1135.

Until recently *P. atrox* was known in the literature from the holotype from Sumatra and from two further examples reported from southern Thailand by Kloss (1916 : 12). The first record for Malaya is of a subadult from the Ulu Gombok Forest Reserve, Selangor, at 2000 ft, reported by Medway (1969 : 43). This second Malayan specimen agrees exactly with those from southern Thailand.

Measurements : length of forearm 34·2 ; greatest length of skull 15·5 ; condylobasal length 13·7 ; condylocanine length 13·7 ; least interorbital width 3·8 ;

zygomatic width 8·7 ; width of braincase 7·0 ; mastoid width 7·4 ; c^1–c^1 3·6 ; m^3–m^3 5·5 ; c–m^3 6·0 ; length of complete mandible 10·5 ; c–m_3 6·5.

Tadarida johorensis (Dobson, 1873)

Malaya : Pulai, Kelantan, 4°48′ N, 101°57′ E, c. 780 ft. ♂♂ (11 subadult) B.M. 73.632, 636, 638–642, 647, 649–651, ♀♀ (6 subadult) B.M. 73.633–635, 637, 643, 644, 646, 648.

Extant accounts of *T. johorensis* are based on one or other of two specimens. The detailed descriptions by Dobson (1876 : 180, 183, fig. a ; 1877 : 718, 726, fig. 5 ; 1878 : 421, 432) refer to the holotype from Johore, Malaya. Later, Andersen (1907 : 39, 44) described a further specimen from Soekaranda, Deli, Sumatra and gave an account of the features of its skull and dentition. These remained apparently the only known specimens until Chasen (1940 : 59) recorded the species from Selangor, Malaya and from the island of Sri Buat, off the east coast of Johore. More recently, Medway & Yong (1969 : 33) have recorded the material from Kelantan on which these notes are based, but as *T. plicata*.

Dobson and Andersen in their descriptions of this species emphasize the large interaural pocket which can be closed by an extension of the interaural band. The inner or anterior margins of the ears are joined by a thick, deep band of integument originating from a low transverse ridge on the muzzle, its upper margin elevated between the ears in a truncately triangular flap. Posteriorly the lower part of this band forms the anterior wall of a deep subtriangular or subquadrangular pocket between the ears, its lateral walls more or less parallel and its posterior wall a low, slightly curved ridge. The pocket is divided by a low median septum and contains a few long hairs at the bottom of its anterior part : otherwise the integument forming and surrounding the pocket is naked or nearly so. The free upper part of the interaural band is convex anteriorly, hollowed posteriorly, and forms a lid or cover to the pocket. Previous descriptions of this structure refer only to the male. The interaural box in two adult females from Kelantan exactly resembles that of the adult male : there is little variation among the younger examples in the series but in these the posterior wall of the pocket is sometimes less prominent and the pocket a little shallower than in the older specimens. The dorsal pelage of specimens (in alcohol) from Kelantan is uniformly mid-brown, the hairs paler at the extreme base. The ventral pelage is predominantly fawn but is browner at the flanks, this shade extending also to the sides of the throat.

Tadarida johorensis is very similar to *T. plicata* from which it differs chiefly in the presence of the interaural pocket. The small cranial differences separating the two species are admirably summarized by Andersen (1907 : 40) and are confirmed by an adult female from the series from Kelantan. These are the absence of marked cranial ridges in *johorensis*, its low, ill-defined sagittal crest terminating more posteriorly and not extending on to the supraorbital region, with the facial foramen placed farther posteriorly immediately above the narrowest part of the postorbital constriction ; a low rostrum in *johorensis*, with straight or slightly concave rostral profile which contrasts with the more inflated, convex profile of *plicata* ; a shallow narial emargination in *johorensis* which extends posteriorly to a line joining the anterior margins of the anteorbital foramina ; the upper incisors are shorter and more massive in *johorensis* which has shorter upper canines and smaller anterior premolars ($\mathrm{pm}\frac{2}{2}$), with the principal cusp of the second upper premolar (pm^4) less developed.

Measurements of adult specimens from Kelantan (♂ B.M. 73.636, ♀ B.M. 73.635 (forearms only), ♀ B.M. 73.637) : length of forearm 46·7, 49·2, 46·4 ; greatest length of skull 19·6 ; condylobasal length 17·3 ; condylocanine length 16·7 ; least interorbital width 4·6 ; zygomatic width 11·2 ; width of braincase 9·9 ; mastoid width 10·6 ; c^1–c^1 4·7 ; m^3–m^3 8·2 ; c–m^3 6·8 ; length of complete mandible 12·5 ; c–m_3 7·3.

SUMMARY

New records of bats from the mainland and islands of south-eastern Asia include the first reports of *Rhinolophus pusillus* Temminck, 1834 (probably conspecific with *R. blythi* Andersen, 1918, which it antedates) from Malaya and the island of Tioman, and of *R. acuminatus acuminatus* from Malaya. *Chironax melanocephalus*, *Myotis horsfieldii horsfieldii* and *Miniopterus medius macrocneme* are recorded for the first time from Sulawesi. Further specimens of *Pipistrellus circumdatus* are recorded from Java and the first Malayan example of this species is reported in detail. The first male specimen of *Philetor brachypterus verecundus* is described from Malaya and a further specimen of *Phoniscus atrox* reported from that country. A series of *Tadarida johorensis* from Kelantan is reported and establishes the presence of the interaural pocket, hitherto known only from the adult male, in female and young examples.

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THE *HAPLOCHROMIS* SPECIES (PISCES : CICHLIDAE) OF LAKE RUDOLF, EAST AFRICA

By P. H. GREENWOOD

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INTRODUCTION

LAKE RUDOLF is outstanding amongst the Rift Valley Great Lakes of Africa for the paucity of its endemic cichlid species, and particularly for the absence of a *Haplochromis* species flock (Trewavas, 1933). Whereas all other large Rift Valley lakes have a well-defined flock of endemic *Haplochromis* species (even if, like Lake Albert, the flock comprises only a few species), Lake Rudolf was thought to possess but a single *Haplochromis* species, the endemic *H. rudolfianus* Trewavas, 1933. The lake's one positive ichthyological peculiarity, the presence of an endemic species belonging to the west African genus *Pelmatochromis*, has now been shown to stem from a misidentification. The Rudolf *Pelmatochromis* is, in fact, a specimen of the widespread taxon *Hemichromis bimaculatus* Gill (*see* Trewavas, 1973).

Endemicity amongst the non-cichlid species is also at a low level (*see* Worthington & Ricardo, 1936 ; personal observations on collections recently made in the lake).

Various ideas have been advanced to explain the absence of a *Haplochromis* species flock in Lake Rudolf (*see* summaries and comment in Fryer and Iles, 1972). Of these, the most likely would seem to be the relative youth of the present lake fauna, an invasion from the Nile in post-Middle Pleistocene times. Coupled with this factor are the shape and recent history of the lake basin, neither of which would provide opportunities for the isolation (and subsequent speciation) of populations living in the lake. That until now the only *Haplochromis* known to inhabit the lake was of a structurally and ecologically generalized type similar to the fluviatile species of eastern Africa, would seem to agree with such a postulated lake history.

Recently, however, a second and anatomically specialized species has been discovered in the deeper waters of the lake. A few specimens of a third species (similar to *H. rudolfianus*, *see* p. 150) have also been collected, and there are indications of yet another taxon (*see* p. 149).

These and other specimens, made available through the efforts of the Lake Rudolf Fishery Research Project, have provided sufficient material to describe the new deep-water taxon, the new *Haplochromis rudolfianus*-like fish, and to redescribe in greater detail *H. rudolfianus* itself. Unfortunately the putative fourth species is represented by so few and distorted specimens that I consider it inadvisable to describe it at present. Nevertheless, sufficient information has been gathered from these few specimens to show that this species too is like *H. rudolfianus*.

As part of a planned review of phyletic relationships within the *Haplochromis*-group cichlids, some consideration is also given to the relationships of the Lake Rudolf species with those of other lakes, especially Lakes Albert and Victoria.

Haplochromis rudolfianus Trewavas, 1933

(Text-figs. 1–4)

Haplochromis rudolfianus Trewavas, 1933, *J. Linn. Soc.* (*Zool.*), **38** : 321–322.

LECTOTYPE. A specimen, 51·0 mm standard length (BMNH reg. no. 1933.2.23 : 163), from a weedy lagoon on the east shore of Lake Rudolf, near Mt El Moitat (station number 285, *see* Worthington, 1932). The specimen has been eviscerated, but judging from its preserved coloration it is probably an adult male.

PARALECTOTYPES. Three specimens (BMNH reg. nos. 1933.2.23 : 164–166), 39·0–42·5 mm S.L., from the same locality as the lectotype (all are eviscerated), and one other specimen (BMNH reg. no. 1933.2.23 : 167), 45·0 mm S.L. from Central Island (Worthington's station no. 264). This latter fish is also eviscerated but is probably an adult male.

Comment on the original description of H. rudolfianus

Trewavas' (1933) original description was based on 5 syntypes, but 25 other specimens were also examined although not included in the description. I have re-examined these fishes and would confirm their identification as *H. rudolfianus*. Dr Trewavas also included in this species, but with certain reservation, a larger specimen, 61·0 mm S.L. and 80 mm total length (BMNH reg. no. 1933.2.23 : 169). The locality label for this fish reads '? Lake Rudolf', the uncertainty stemming from the collector's notes on the provenance of the specimen. A number of differences between this fish and other specimens of *H. rudolfianus* were noted by Trewavas. I can confirm these differences and would add others. The size discrepancy once existing between this specimen and others of *H. rudolfianus* is virtually obliterated by the larger specimens of the latter species now in the Museum's collections. Thus it seems very unlikely that the various differences listed by Trewavas are, as she then suggested, size correlated ones.

The specimen in question departs from *H. rudolfianus* in having a deeper body (37·4 per cent of standard length), somewhat deeper preorbital (17·7 per cent of head length), wider interorbital distance (25·6 per cent of head), a deeper cheek (25·6 per cent of head), a smaller eye diameter (30·0 per cent of head) and a markedly shorter caudal peduncle (14·7 per cent of standard length, *cf.* 16·5–19·7, mean 18·0 per cent in *H. rudolfianus*). The fish also differs from specimens of *H. rudolfianus* in having fewer gill rakers (7 *cf.* 8 or 9), larger scales on the nape and in the lateral line series (30), in lacking the characteristic dark vertical bars on the body and caudal peduncle (*see* p. 147), in having no melanic pigment in the ovarian walls (*see* p. 146) and in having stouter and somewhat obliquely cuspidate outer jaw teeth. The lower pharyngeal bone is finer than in *H. rudolfianus*, and the median lower pharyngeal teeth are also finer (*see* p. 146).

In my opinion, this specimen cannot be identified as a member of *H. rudolfianus*, nor can it be placed in either of the other *Haplochromis* species from Lake Rudolf. All the evidence certainly suggests that it in fact belongs to the fauna of another lake. On this assumption, the specimen was compared with *Haplochromis* species from all the lakes sampled by the Cambridge University Expedition of 1930–31. It cannot be identified with any known Lake Albert *Haplochromis* species, nor does it closely resemble any of the described (or known but undescribed) species of Lakes Edward and George; *see* Greenwood, 1973. It does, however, closely agree in all morphometric and anatomical features (especially the dentition) with *H. velifer* Trewavas of Lake Nabugabo, Uganda (*see* Greenwood, 1965). Since extensive collections were made in this lake by the Cambridge Expedition, I would identify the fish as a specimen of *H. velifer* and suggest that the locality label be altered to read 'Lake Nabugabo'.

The redescription of H. rudolfianus given below is based on the 5 type specimens (39·0–51·0 mm S.L.) and 20 additional fishes (30·5–58·0 mm S.L.) collected in 1972 by the Lake Rudolf Fisheries Research Project team at Topi point, Allia Bay, and Ferguson's Gulf. Coloration and certain anatomical details were also checked on the other specimens from which meristic and morphometric data were not taken (BMNH reg. nos. 1973.11.13 : 151–170).

All counts and measurements used in this description are those defined by Greenwood (1973).

Dorsal head profile straight or gently curved, sloping at an angle of 25–30 degrees with the horizontal; premaxillary pedicels rarely breaking the smooth outline of the profile.

Length of head 31·0–35·3 (mean, M = 33·5) per cent of standard length, depth of body 29·4–33·7 (M = 32·1) per cent.

Preorbital depth 12·5–17·9 (M = 15·0) per cent of head, least interorbital width 20·0–27·4 (M = 22·7) per cent, neither dimension showing allometry with standard length. Length of snout 26·6–32·3 (M = 29·9) per cent of head, 0·7–1·1 (mode 0·8) times its breadth. Eye diameter 30·5–35·7 (M = 32·9) per cent of head (showing ill-defined negative allometry), depth of cheek 17·4–25·8 (M = 21·7) per cent.

Caudal peduncle 16·5–19·7 (M = 18·0) per cent of standard length, 1·2–1·7 (modal range 1·3–1·5) times as long as deep.

Mouth horizontal or slightly oblique. Length of upper jaw 30·8–38·0 (M = 33·7) per cent of head, length of lower jaw 35·7–48·3 (M = 39·7) per cent, 1·4–1·8 (modal range 1·5–1·7) times as long as broad. Posterior tip of maxilla reaching a vertical through the anterior margin of the eye.

Gill rakers. Relatively stout, with the lower 1 or 2 on the first gill arch reduced; 9 (less frequently 8, rarely 10) on the lower limb of that arch. Well-developed 'pseudorakers' (fleshy protuberances between the inner and outer row of true rakers) are present on the first arch.

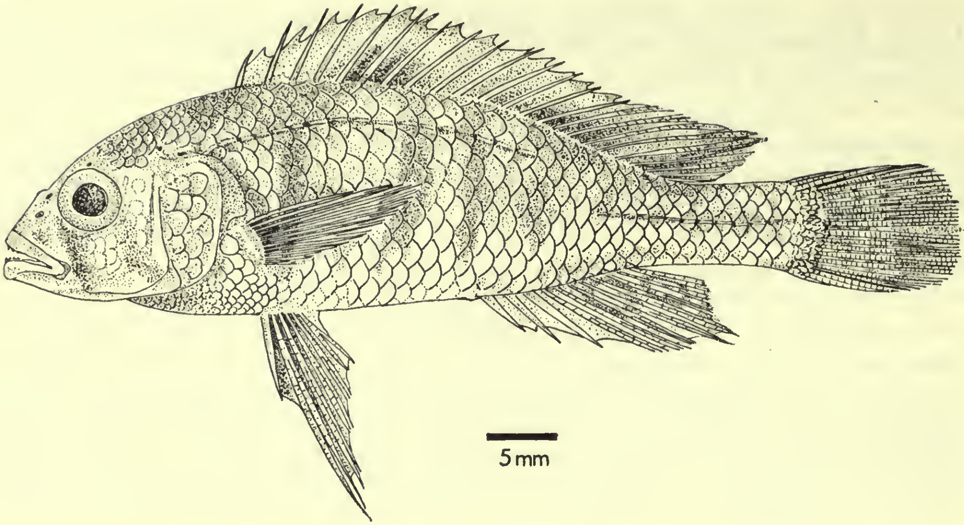

FIG. 1. *Haplochromis rudolfianus*. Lectotype. Drawn by Gordon Howes.

Scales. Strongly ctenoid, those on the anteroventral aspects of the thoracic region very small, with an abrupt size transition between them and the posterior scales of this region. Immediately anterior to the first dorsal fin spine there is a small naked area (about 1½ or 2 scales in area), and often there is also a narrow naked strip below the ventral horizontal row of cheek scales. Lateral line with 30 (f2), 31 (f10), 32 (f12), or 33 (f1) scales, cheek with 3 (rarely 2 or 4) rows. Six or 7 scales between the dorsal fin origin and the upper lateral line, 6 or 7 (rarely 5) between the pectoral and pelvic fin bases.

Fins. Dorsal with 24 (f12), 25 (f11) or 26 (f2) rays, comprising 14 (f3), 15 (f21) or 16 (f1) spinous and 9 (f9), 10 (f15) or 11 (f1) branched rays. Anal with 3 spinous and 8 (f3), 9 (f20), 10 (f1) or 11 (f1) branched rays.

First branched ray of the pelvic fin very slightly produced in both sexes, but relatively more so in adult males.

Caudal subtruncate, scaled on its basal quarter to third.

Teeth. The majority of teeth in the *outer row* of *both jaws* are unequally bicuspid and moderately stout (Text-fig. 2); the major cusp is acutely pointed and equilateral in outline. A few unicuspid teeth sometimes occur posteriorly in the upper jaw, but more often the posterior teeth are tricuspid; rarely are these teeth bicuspid. A noteworthy feature of the samples examined is the pronounced wear pattern seen on the outer teeth. Worn teeth have the major cusp either obliquely truncate or the wear may be so great that all demarcation between major and minor cusps has disappeared and the crown is spatulate.

There are 28–48 teeth in the outer premaxillary row, the number showing some positive correlation with the fish's length.

All *inner row* teeth are small tricuspids, and are arranged in 2 or 3 (mode), rarely 4, rows in the upper jaw and in 2 (mode) or 3 rows, rarely a single row, in the lower jaw.

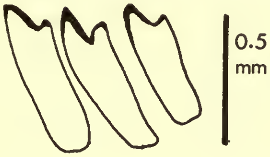

FIG. 2. *Haplochromis rudolfianus.* Outer row jaw teeth (in labial view) from left dentary, anterolateral in position.

OSTEOLOGY. The *neurocranium* (Text-fig. 3A) of *H. rudolfianus* is of the generalized '*H. bloyeti*'-type (see Greenwood, 1974), with a moderately decurved profile and a relatively short preotic skull length (*ca* 62·5 per cent of total neurocranial length). None of the cephalic laterosensory canals or pores, nor any of the bones carrying the canals, is at all hypertrophied (*cf.* p. 155 ; Text-fig. 3B).

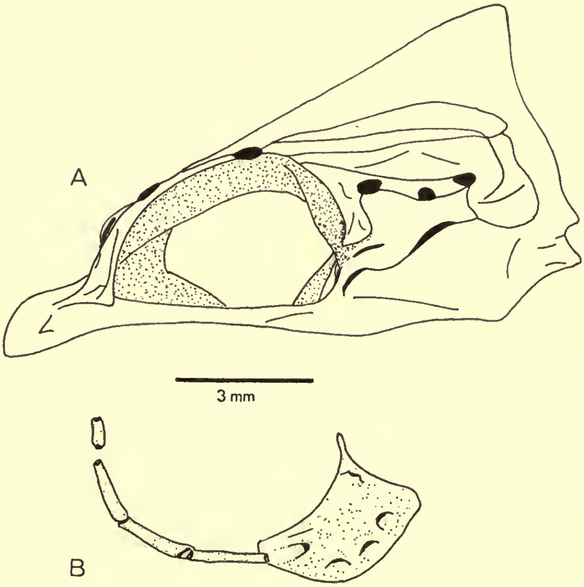

FIG. 3. *Haplochromis rudolfianus.* A : Neurocranium, left lateral view. B : Bones in the infraorbital series of the right side.

The *lower pharyngeal bone* (Text-fig. 4) is triangular in outline, with the dentigerous area a little broader than long (*ca* 1·1 times). In all specimens examined the bone is noticeably stout, especially compared with that of the other Rudolf species or that of the generalized species in other lakes and in the east African rivers. The degree of enlargement, however, varies between individuals.

The two median tooth rows are composed of teeth clearly stouter than their lateral congeners; the degree of enlargement, like that of the bone itself, shows considerable individual variability. All five specimens in the type series have the stoutest bones and dentition of all the specimens examined; the lectotype (51 mm S.L.) is exceptional even amongst the type series in having submolariform teeth posteriorly in the median rows (in all other specimens the bicuspid crown is still retained). The lectotype also has the relatively most massive lower pharyngeal bone (Text-figs. 4A and B).

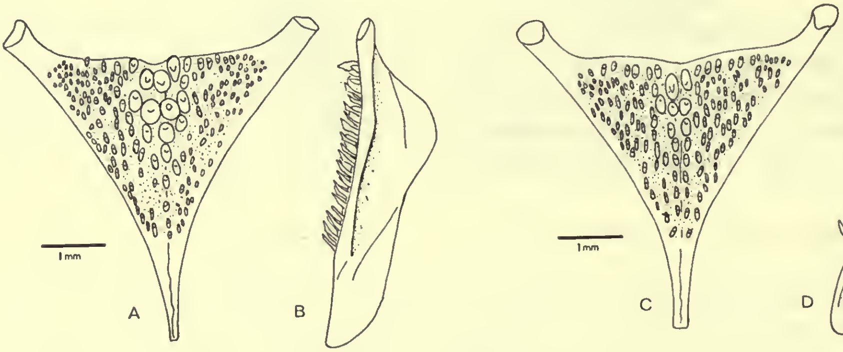

FIG. 4. *Haplochromis rudolfianus.* Lower pharyngeal bones to show variation in size of median teeth. A and B: Bone from one of the paratypes, in occlusal and left lateral views respectively. C and D: Bone from another specimen of the same size, in occlusal and left lateral views respectively.

Lower pharyngeal bone and tooth enlargement does not seem to be size correlated because some of the syntypes are amongst the smaller fishes examined, and a specimen 7 mm longer than the lectotype has a less massive bone and dentition.

Vertebral counts in the 30 specimens radiographed are: 27 (f1), 28 (f3), 29 (f18) or 30 (f8), comprising 11 (f1), 12 (f4), 13 (f23) or 14 (f2) abdominal and 16 (f23) or 17 (f7) caudal vertebrae. (The fused first ural and preural centra are not included in these figures.)

Only two specimens show any sign of fusion or close apposition between elements in the hypural series (*cf.* p. 158); in these two fishes the first and second hypurals seem to be fused.

VISCERA. The intestine is from $1\frac{1}{3}$ to $1\frac{1}{2}$ times the standard length; the ovaries are of unequal size with the right ovary noticeably larger than the left in most specimens or, rarely, it alone shows signs of oogenesis. A very characteristic feature is the intensely melanic tissue of the ovary wall; the testes, however, are but slightly pigmented. The entire peritoneum is also densely melanic. This extreme visceral melanism is probably correlated with the intense sunlight to which fishes living in the shallows of Lake Rudolf would be subjected.

COLORATION. In freshly killed specimens of *adult male H. rudolfianus* the ground colour is greenish-yellow (but whitish on the chest). Dark vertical bars cross the flank and caudal peduncle (*see* notes on preserved colours below). Each scale on the flanks has an opalescent centre in which yellow, blue and green colours can be detected ; yellowish pigment predominates on the anterior body scales, especially those around the base of each pectoral fin. Posteriorly on the body the dominant colour in the scale centres is electric blue, and is especially noticeable around the base of the anal fin. The head, like the anterior part of the body, is an opalescent greenish-yellow and blue, the operculum marked with a golden yellow area on its lower part. The branchiostegal membrane is a delicate pale yellow except for a clearly demarcated black area anteriorly.

The dorsal fin membrane is dark golden-yellow, the lappets are scarlet and the soft part of the fin has a bright yellow basal streak and light yellow dots dorsally, the intervening areas melanic. Black spots also occur on the spinous part of the fin. Two dark basal blotches occur on the spinous dorsal ; the first lies between the sixth to ninth spines, the second between the last two or three spines. The anal fin is yellow but with scattered black and red chromatophores, and with two or three light golden-yellow ocelli. The caudal is a marbled yellowish-green, with red and black spots, the red colour being most intense in the dorsal and ventral angles of the distal margin. The pelvic fins are dusky.

Adult females have a similar but more subdued coloration, with the whitish ventral areas more extensive and without the black anterior region to the branchiostegal membrane. The pelvic fins are hyaline tinged with yellow, and the red lappets and margin to the dorsal and anal fins respectively are barely discernible. On the anal fin there are pale yellow spots in the same position as the ocelli of males.

I am indebted to Mr and Mrs Hopson for supplying the notes on which this description is based.

Preserved coloration is virtually identical in both sexes, except that the pelvics in females are clear and not dusky, and the ground coloration is lighter than in males.

The ground coloration is a pale brown (fawn) shading to greyish-charcoal on the chest and belly. The flanks and caudal peduncle are crossed by 5–7 (rarely 8–10) dark and clearly defined vertical bars ; the bars on the flanks reach almost to the ventral profile, but those on the caudal peduncle rarely extend to below the level of the midlateral line where they merge with a short and faint horizontal bar extending the length of the peduncle. This bar is of variable intensity and is barely visible in some specimens. Anteriorly there is a broad, sometimes ill-defined dark bar overlying the cleithrum and following the outline of that bone ; dorsally the bar joins a dark, saddle-shaped blotch on the nape. A fainter bar is sometimes visible along the vertical limb of the preoperculum. The snout is crossed by a pair of parallel dark bars, and there is an intense and clearly demarcated lachrymal stripe.

All fins are a greyish-hyaline, the soft dorsal and the entire caudal are maculate, the dorsal with two distinct dark blotches basally (*see above*), and with dark lappets. Spotting on the caudal fin is most distinct proximally, the spots often arranged so as to produce two to four dark vertical bands on that part of the fin. The pelvics are dusky in males, greyish in females.

ECOLOGY. *Haplochromis rudolfianus* is apparently confined to the shallow and protected inshore areas of the lake, although there is a population inhabiting a crater lake on Central Island (*see below*). No data are yet available on the feeding habits of this species, nor whether it shows any particular substrate preferences.

Males appear to reach a larger size than do females, and are adult at a standard length of 45–47 mm. Females, however, mature at a smaller size, namely *ca* 30 mm. No data are available on the breeding habits or seasons of the species.

THE CENTRAL ISLAND POPULATION. One of the paralectotypes (*see* p. 142) and 12 additional specimens collected in 1965 by Dr R. L. Welcomme are from Central Island. The paralectotype is apparently from the shore of the island (station no. 264, *see* Worthington, 1932) but the other fishes are from one of the crater lakes in that island (*see* Beadle, 1932, for details of the lakes).

The Central Island fishes, particularly those from the crater itself, are of considerable interest since they are apparently isolated from other populations inhabiting the mainland shores of the lake. The apparent absence of *H. rudolfianus* from open-water localities suggests that it does not leave (or at least not frequently) its shallow-water inshore habitats.

A population of *Sarotherodon* living in Crater Lake A of Central Island is sufficiently distinctive for it to have been referred to a new species (*Tilapia vulcani*, Trewavas, 1933, *see also* Trewavas, 1973, for distinguishing features of the genera *Tilapia* and *Sarotherodon*). A population from the neighbouring Crater Lake C, however, did not differ significantly from the populations of *Sarotherodon niloticus* living in the main lake (Trewavas, 1933). The explanation for this seemingly anomalous situation appears to be that Lake C is, on occasion, connected with the main lake. (Personal communication from Dr K. E. Banister, based on information he was given by members of the Fishery Research Team on Lake Rudolf ; the last interconnection was in 1972.) Lake A, on the other hand, is completely isolated from the main lake by a crater wall at least 10 m above current lake level.

It is the more regrettable then that the *H. rudolfianus* collected in 1965 bear no more precise locality data than 'Crater Lake, Central Island', and that all are distorted and poorly preserved. Allowing for the difficulty of measuring distorted specimens, I can find no meristic or morphometric differences between the Central Island fishes and those from the main lake. Several of the Island fishes are, however, larger than any recorded from the lake (maximum size 72 mm, *cf.* 58 mm for lake fishes). The largest Island fish has four or five unicuspid teeth situated posterolaterally in the upper jaw, but this could well be a size-correlated phenomenon (*see* Greenwood, 1974). Most of the Island fishes are much darker than are the lake fishes and consequently the vertical barring on the body is less obvious ; in a few paler individuals, however, the bars are quite distinct. Like their main lake congeners, female Crater Lake fishes have only the right ovary well developed, but unlike the latter populations the ovarian wall in these fishes is but faintly melanized and then only on the dorsal and lateral aspects. These observations were paralleled by those I was able to make on specimens and colour photographs obtained by Dr Banister during his recent visit to the lake. Once again, the specimens are not well preserved and add little anatomico-morphological information to that already available.

However, the similarity in coloration between Dr Banister's fishes from Crater Lake A and those from the Welcomme sample strongly indicate that the latter are from the same source.

The dark coloration of Central Island *H. rudolfianus* seems to parallel that of '*Tilapia vulcani*' from Crater Lake A on the island (*see* Trewavas, 1933). In other characteristics the parallelism is not clearly apparent. That is to say, the *H. rudolfianus* specimens do not show the leanness, larger eyes, larger heads, longer dorsal fin spines and broader bands of inner teeth that Trewavas noted in the *Tilapia* specimens (Trewavas, 1933).

In contrast to the Central Island Crater Lake A specimens of *H. rudolfianus*, the paralectotype from the shore of the island does not show any marked darkening of the ground coloration. Unfortunately, it is eviscerated so no check can be made on the melanization of its gonads. The peritoneum is very dark.

Without more precise locality data, more material from different localities on the island and more details on live coloration, little can be said about the taxonomic status of Central Island populations of *H. rudolfianus*. It does, however, seem probable that, like the Crater Lake A population of *Sarotherodon niloticus* (with which species '*T. vulcani*' should now be synonymized; Dr Trewavas, personal communication), the Crater Lake A *Haplochromis* show some ecophenotypic response to their peculiar environment. The relative melanism shown by Crate Lake A *Haplochromis rudolfianus* populations is of particular interest because male coloration seems to be an important species recognition character (*see* Greenwood, 1974). Altered male coloration apparently is one of the first morphological differences seen in recently speciated *Haplochromis* (Greenwood, 1965).

DIAGNOSIS AND AFFINITIES OF *H. rudolfianus*. The distinctively barred colour pattern of this species immediately serves to distinguish it from all other *Haplochromis* species in Lake Rudolf (*see* footnote, below). From *H. macconneli* described on p. 154, *H. rudolfianus* is further distinguished by the absence of hypertrophied laterosensory canals and pores on the head, by several morphometric characters (*see* p. 155) and in having few, if any tricuspid teeth in the outer series of either jaw. In addition to the hypertrophied canal system, the neurocranium in *H. macconneli* is of a more derived type than that of *H. rudolfianus*. The nearest living relatives of *H. rudolfianus* are probably *H. turkanae* (see p. 153), and the fourth but as yet undescribed *Haplochromis* species in the lake.[1]

The validity of these relationships can only be tested when more material of the putative relatives is available.

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[1] Four specimens 37·0–64·0 mm standard length (and a fifth prepared as a skeleton) may represent a fourth *Haplochromis* species. Morphometrically these fishes are not distinguishable from *H. rudolfianus*, and the dentition is similar except for there being only a single row of inner teeth in each jaw. The principal 'interspecific' difference seems to be in the coloration, both that observed by Mr Hopson (*in litt.*) when the fishes were alive and that remaining in the preserved material. There is also an observable (but non-quantifiable) difference in head shape, and these fishes have a colourless (not black) peritoneum. The gonads show no sign of melanization, unlike those of *H. rudolfianus*.

All five specimens are from water between 15 and 35 m deep; that is, from somewhat greater depths than *H. rudolfianus*, but within the range of *H. turkanae*, from which species they differ in the same morphometric characters as does *H. rudolfianus*.

Since only five specimens are available and because all are in some way damaged or distorted, I would consider it inadvisable to describe a new taxon on this material.

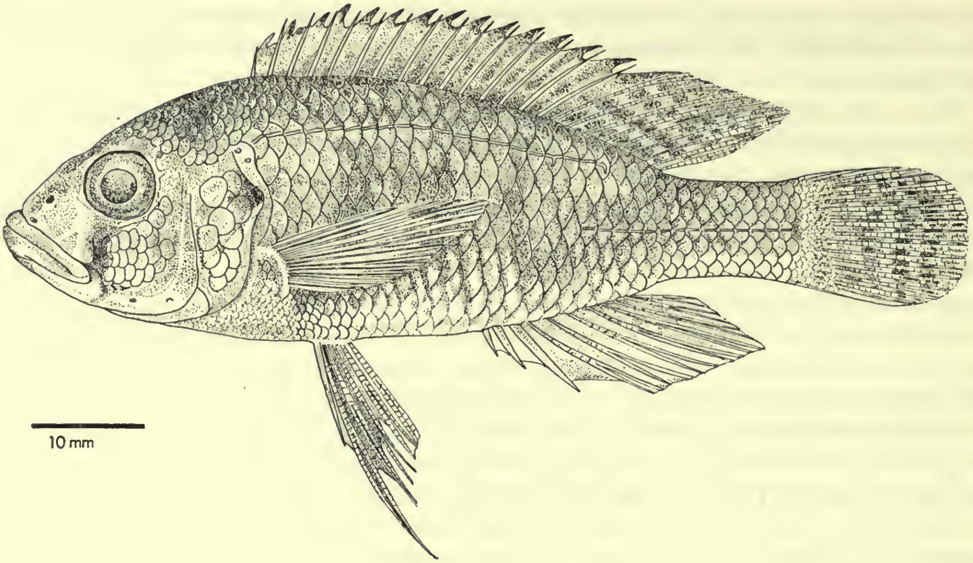

FIG. 5. *Haplochromis turkanae.* Holotype. Drawn by Gordon Howes.

In its gross morphology and in the details of its pectoral and predorsal squamation, *H. rudolfianus* resembles *H. albertianus* Regan, a species endemic to Lake Albert (*see* Trewavas, 1938). The two species differ in their preserved colour patterns, and in adult *H. albertianus* (of the same size as *H. rudolfianus*) having unicuspid outer jaw teeth and a more massive lower pharyngeal bone with a greater number of enlarged, submolariform teeth. In other words, *H. albertianus* shows a greater degree of specialization in those characters that are already somewhat specialized in *H. rudolfianus*.

STUDY MATERIAL

Register number BMNH	Locality : Lake Rudolf
1973.11.13 : 151–154	Ferguson's Spit (shallow water, inshore)
1973.11.13 : 155–170	Topi Point, Allia Bay

Haplochromis turkanae sp. nov.

(Text-figs. 5 and 6)

HOLOTYPE. An adult male, 73·0 mm standard length (BMNH reg. no. 1973.11.20 : 1), caught in a bottom trawl fished at a depth of 16 m, over a mud and rock bottom, 5·6 km north-west of Porr.

PARATYPES. Three adult males (BMNH reg. nos. 1973.11.20 : 2–4), 77·5–86.0 mm S.L. from the same locality and trawl as the holotype.

DESCRIPTION. Based on these four fishes, 73·0–86·0 mm S.L. With so few specimens available most of the morphometric data can be presented most conveniently in tabular form.

S.L.	Depth*	Head*	PO %	IO %	Snt %	Eye %	Cheek %	Lj %	Uj %	CP*
73·0	35·0	33·5	20·5	20·5	30·6	28·6	28·6	45·0	41·0	17·5
77·5	35·0	32·3	18·0	22·0	32·0	30·0	32·0	44·0	40·0	17·4
81·0	34·5	32·7	18·9	20·8	34·0	34·0	26·4	45·3	41·5	18·5
86·0	33·2	31·4	18·5	22·0	29·6	27·9	27·0	44·5	40·8	16·9

* = per cent of standard length. % = per cent of head length.
PO = preorbital depth; IO = least interorbital width; Snt = snout length; Lj = lower jaw, and Uj = upper jaw length. CP = caudal peduncle length.

Caudal peduncle 1·4–1·5 times longer than deep. Dorsal profile of head straight or gently curved dorsally, but straight anteriorly, sloping at an angle of 30–35 degrees with the horizontal. The ascending processes of the premaxillae barely interrupt the outline of the profile.

Mouth slightly (but noticeably) oblique, the lips a little thickened; posterior tip of the maxilla reaching a vertical through the anterior part of the eye. Jaws equal anteriorly, the lower 1·6–1·7 times longer than broad. Snout broader than long, its anterior profile, when viewed from above, smoothly rounded. None of the cephalic laterosensory canals (or their pores) is noticeably enlarged.

Gill rakers. Relatively stout, 8 (f3) or 9 (f1) on the lower part of the first arch, the lowermost one or two rakers reduced in size. Pseudorakers (*see* p. 143) are developed between the inner and outer rows of gill rakers, but are not conspicuous.

Scales. Ctenoid; lateral line with 31 (f3) or 32 (f1) scales, cheek with 4 (f1) or 5 (f3) imbricating rows. Six or 7 scales between the upper lateral line and the dorsal fin origin; a naked area (about 1½ scales in extent) immediately before the first dorsal fin spine. Nine or 10 scales between the pectoral and pelvic fin bases; the scales of the chest are also very small and grade abruptly with the larger scales of the post-pectoral region.

Fins. Dorsal with 14 (f2) or 15 (f2) spinous rays and 9 (f4) branched rays, anal with 3 spines and 7 (f2) or 8 (f2) branched rays. The first pelvic ray is produced, very noticeably so in two specimens where it extends as far as the second branched anal ray. The caudal fin is strongly subtruncate, almost rounded, and scaled on its proximal quarter to half. Pectoral fin 25·6–28·7 per cent of standard length, 81·5–88·0 per cent of head length.

Teeth. In all four specimens the posterior three or four teeth in the *outer premaxillary row* are strong, dagger-like unicuspids. In two fishes the other teeth in this row are a mixture of caniniform unicuspids and weakly bicuspids, while in the other two specimens distinctly bicuspid teeth predominate, although a few unicuspids occur anterolaterally. There are 42–52 teeth in this row. There is a similar difference in the predominant tooth type of the outer row in the *lower jaw*. The first two specimens have mainly unicuspid teeth with a few bicuspids, the second

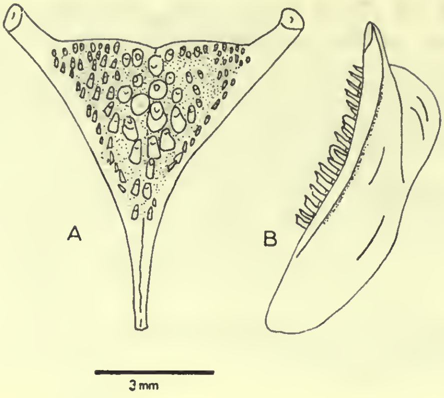

FIG. 6. *Haplochromis turkanae.* Lower pharyngeal bone of holotype in A : occlusal view ; B : left lateral view.

pair have a predominance of bicuspids. Bicuspid teeth in the lower jaw have their crowns more distinctly incurved than do the upper jaw teeth.

Bicuspid teeth in both jaws are of the typical generalized *Haplochromis* type, and closely resemble the teeth of *H. rudolfianus* (*see* p. 144 ; Text-fig. 2).

The *inner series* of teeth in both jaws are composed of small tricuspids arranged in 3 rows in the upper and 2 (or irregularly 2) rows in the lower jaw.

OSTEOLOGY. With only four specimens available, no skeletal preparations were possible. Vertebral counts made from radiographs are : 28 (f3) and 29 (f1), comprising 13 abdominal and 15 or 16 caudal vertebrae (the fused first preural and ural centra not included). No specimen has any fused elements in the caudal fin skeleton, but in two fishes hypurals 1 and 2 are closely apposed.

COLORATION. No information is available on the live colours of this species. The four adult (but not sexually active) male specimens (fixed in formalin) have a light grey to yellowish-grey ground colour that extends ventrally to a clearly demarcated horizontal line on the body and caudal peduncle, at which level it becomes pearly white. The line is at about the horizontal level of the lowermost insertion of the pelvic fin ; thus in lateral view little of the caudal peduncle shows the white ventral coloration. On the flanks, most dorsal, lateral and ventrolateral scales have a narrow margin of dark pigment. The lower jaw, branchiostegal membrane, suboperculum and the lower part of the cheek are also pearly-white.

About five very faint vertical dark bars are visible on the flanks, and another may also occur posteriorly on the caudal peduncle ; these bars are narrower dorsally than ventrally, and do not extend onto the white ventral coloration of the body. The vertical limb of the preoperculum is faintly to clearly dusky and there is a broad, intensely black lachrymal bar that, at about the level of the posterior maxillary tip, narrows abruptly and then continues ventrally and a little medially onto the lower jaw.

The entire soft dorsal fin and the posterior half of the spinous dorsal are densely and distinctly spotted, with the spots arranged in from four horizontal rows anteriorly to six or more rows posteriorly on the fin. On the anterior part of the spinous dorsal the spots are confluent and form vertically aligned, dark, interspinous streaks. The lappets of the dorsal fin are black. The entire caudal fin is covered with dark and discrete spots so arranged as to form wavy, vertical bars when the fin is not fully opened. The anal is hyaline except for three rather pale ocelli. The pelvics have the anterior half dusky, the posterior half hyaline ; the elongate first pelvic ray is dead-white.

ECOLOGY. Virtually nothing is known about the biology of this species. The four specimens came from deeper water than is usual for *H. rudolfianus*, and shallower water than is usual for *H. macconneli* (*see* pp. 148 and 159).

All four specimens have the stomach and intestine packed with fragments of ostracod shells.

It is interesting to note that, unlike *H. rudolfianus* but like *H. macconneli*, there is no trace of dark pigment in the peritoneum and neither is there any on the gonads (*cf.* p. 146).

All four specimens are adult males, but judging from the size and shape of the testes, none is sexually active.

DIAGNOSIS AND AFFINITIES. *Haplochromis turkanae* is immediately distinguishable from *H. macconneli* because of its non-hypertrophied cephalic laterosensory canal system. There are also morphometric differences between the species, differences in their dentition and, apparently, in the preserved coloration of adult males (*see below*, pp. 156–159).

In its general appearance, its dentition and in several morphometric characters, *H. turkanae* closely resembles *H. rudolfianus*. It differs principally in having more rows of scales on the cheek (4 or 5, *cf.* 3), smaller scales between the pectoral and pelvic fin insertions (9 or 10, *cf.* 6 or 7), a deeper cheek (26·4–32·0 per cent of head, *cf.* 17·4–25·8, M = 21·7 per cent), longer upper jaw (40·8–41·5, *cf.* 30·8–38·0, M = 33·7 per cent of head), and a somewhat longer lower jaw (44·0–45·3, *cf.* 35·7–48·3, M = 39·7 per cent of head). *Haplochromis turkanae* also differs in having a more elongate first pelvic ray (which is distinctively coloured) and in its overall coloration. For example, it lacks the prominent vertical bars on the body, has more intensely and densely maculate dorsal and caudal fins, and has the peculiar dribble-like extension of the lachrymal bar onto the lower jaw. The lower pharyngeal bone and dentition of *H. turkanae* are somewhat more massive than those of most *H. rudolfianus*, but are quite comparable with those in the type series of that species (*see above*, p. 146, and *cf.* figs. 4 and 6).

Without more osteological information on *H. turkanae* it is difficult to say much about its affinities with *H. rudolfianus*. From what is known, however, the two species would seem to be very closely related phyletically. Indeed, the resemblance parallels that seen between many pairs of *Haplochromis* species in Lake Victoria. As in many of the Victoria pairs there is also an apparent ecological replacement involved, with *H. rudolfianus* being the inshore, shallow-water species and *H. turkanae* the species of deeper waters (*see* Greenwood, 1974).

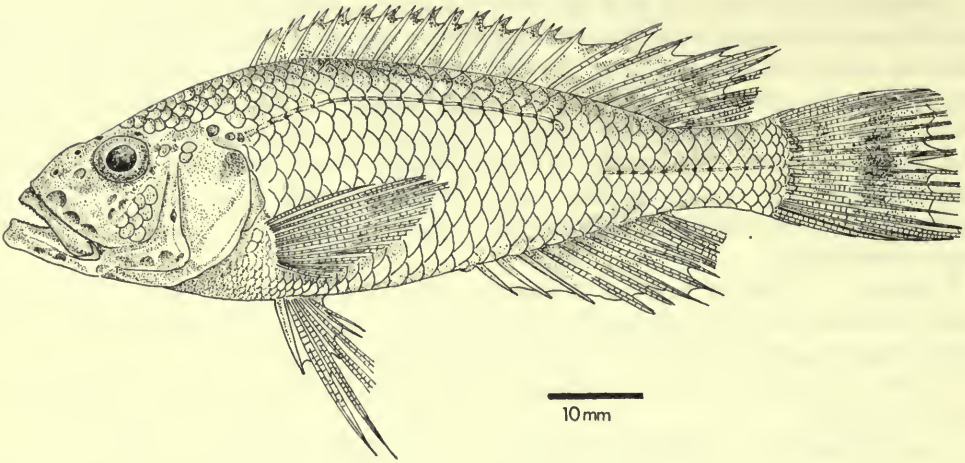

FIG. 7. *Haplochromis macconneli.* Holotype. Drawn by Gordon Howes.

Haplochromis macconneli sp. nov.

(Text-figs. 7–10)

This most distinctive species was discovered by Mr and Mrs A. J. Hopson when the Lake Rudolf Research Project team began trawling operations in the deeper waters of the lake. Apparently it is confined to water more than 20 m deep and has been collected from depths down to 75 m.

Besides its various anatomical peculiarities, *H. macconneli* is also noteworthy for its marked sexual dimorphism in adult size. No males larger than 35·5 mm standard length have yet been recorded. Indeed, despite intensive efforts, only two males have so far been recognized amongst the several hundreds of specimens examined. Females, on the other hand, are common components of deep-water trawl catches.

The taxon is named for Mr R. B. McConnel, Officer in Charge of the Fisheries Department at Lake Rudolf, in grateful recognition of the assistance he has unstintingly given to Mr Hopson and his research team.

HOLOTYPE. A female, 77·0 mm standard length (BMNH reg. no. 1973.11.13 : 37), caught near the bottom in 50–64 m of water 3 miles north-west of Central Island.

PARATYPES. (i) Twenty-one specimens (BMNH reg. nos. 1973.11.13 : 38–58), 51·0–72·0 mm S.L., all females and from the same locality as the holotype ; (ii) 6 juveniles (of indeterminable sex), 22·0–38·0 mm S.L., caught in a bottom trawl at a depth of 20 m 1·6 km off Ferguson's Spit (BMNH reg. nos. 1973.11.13 : 59–64 ; (iii) 2 adult males, 31·0 and 35·5 mm S.L., caught in a bottom trawl at a depth of 30 m, 2·4 km east of North Island (BMNH reg. nos. 1973.11.13 : 65–66).

DESCRIPTION. Based on the holotype and 29 paratypes, 22·0–77·0 mm S.L. Various characters have been checked on the 78 additional specimens (size range 15·0–59·0 mm S.L.) from the Ferguson's Spit station and one other station 3·2 km off-shore at a depth of 75 m. None of this extra material has, however, been included in the morphometric counts and measurements.

Because most of the proportional measurements used in this description show allometry with the fish's size, the material has been divided into two size groups, one of fishes 51–77 mm S.L. and the other of fishes 22–38 mm S.L. Ranges and means for the larger specimens (N = 22) are given first, followed in parentheses by those for the smaller fishes (N = 8).

Length of head 33·3–39·9, M = 35·3 (31·6–39·4, M = 36·0) per cent of standard length, depth of body 31·7–35·1, M = 33·3 (25·3–32·3, M = 29·7) per cent.

Dorsal profile of head clearly but gently concave above the eye, sloping at an angle of *ca* 35–40 degrees to the horizontal. The profile of the snout varies from straight to somewhat decurved, with the premaxillary pedicels always breaking the outline. The anterior tip of the lower jaw is usually produced into a symphysial knob, which is most obvious in fishes over 65 mm S.L.

An outstanding feature of the head (in specimens of all sizes) is the greatly enlarged openings to all the laterosensory canals (Text-figs. 7 and 9). Particularly obvious are those on the preorbital and preopercular bones. The underlying canals are hypertrophied, with the result that the bones involved have a distinctly inflated appearance.

Laterosensory canals on the neurocranium, especially the temporal canal of the pterotic bone, are also inflated, particularly in comparison with those in *H. rudolfianus* and *H. turkanae*, and indeed with those of the generality of *Haplochromis* species (*see below*, p. 158). Canals, and their openings, in the extrascapular and supracleithrum are equally affected by this trend, as are the nasals although the latter are relatively the least cavernous of the cephalic laterosensory canal bones. In well-preserved specimens the canal openings are occluded by a thin membrane.

Depth of preorbital 16·6–22·2, M = 20·1 (12·5–16·7, M = 15·4) per cent of head, least interorbital width 18·8–24·2, M = 21·8 (14·7–25·0, M = 21·2) per cent. Snout slightly broader than long (rarely as long as broad) in specimens of all sizes, its length 27·8–38·1, M = 33·8 (26·1–33·3, M = 29·6) per cent of head for the size groups respectively. Diameter of eye 23·7–29·3, M = 26·8 (25·0–33·3, M = 28·7) and depth of cheek 22·8–29·3, M = 26·7 (18·1–25·0, M = 21·2) per cent of head.

Caudal peduncle 16·5–21·5, M = 18·6 (17·8–22·6, M = 20·0) per cent of standard length, 1·5–2·2 times as long as deep in fishes of all sizes.

Lower jaw with a distinct symphysial knob in fishes of all sizes, the protuberance most marked in individuals of > 65 mm S.L. Length of lower jaw 40·8–51·0, M = 45·6 (37·6–46·2, M = 42·0) per cent of head, 1·6–2·0 (modal range 1·8–2·0) times longer than broad in specimens of all sizes. Length of upper jaw 31·8–44·0, M = 38·4 (30·6–37·6, M = 33·3) per cent of head.

Mouth slightly oblique, the posterior tip of the maxilla reaching a vertical through the anterior margin of the orbit, or to a point slightly posterior to that line.

Gill rakers. Of variable form, but usually with the upper 2 or 3 rakers on the first gill arch flattened and branched, those on the middle section of the arch relatively slender, and the lowermost 1 or 2 rakers reduced ; no pseudorakers are developed

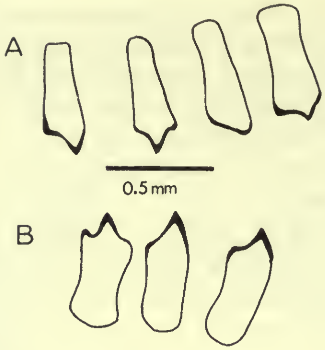

FIG. 8. *Haplochromis macconneli.* Dentition. A: Outer teeth from the premaxilla. B: Outer teeth from the dentary. In both, the teeth are from an anterolateral position in the jaw and are viewed labially.

(*see* p. 143). There are 7 (f1), 8 (f8) or 9 (f21) rakers on the lower limb of the first gill arch.

Scales. Ctenoid, those on the chest very small but grading in size with those on the subpectoral region (that is, the demarcation between small and large scales in this region is less abrupt than in *H. rudolfianus*; *see* p. 154).

Five and a half to 7 (mode 6) scales between the dorsal fin origin and the lateral line, 7–9 (modes 8 and 9), rarely 5, between the pectoral and pelvic fin bases. Cheek with 3 or 4 rows of imbricating scales. In most specimens there is a small naked area (about the area of one scale) in front of the first dorsal fin spine.

Fins. Dorsal with 22 (f6), 23 (f16) or 24 (f8) rays, comprising 13 (f2), 14 (f16), 15 (f11) or 16 (f1) spinous and 8 (f11), 9 (f18) or 10 (f1) branched rays. Anal with 3 spines and 7 (f2), 8 (f25) or 9 (f3) branched rays. First ray of the pelvic fin slightly produced, more so in larger fishes. Caudal truncate, scaled on its proximal quarter (mode) to third. Pectoral fin 25·8–34·5, M = 28·6 (23·7–28·3, M = 26·1) per cent of standard length, and 73·0–92·5, M = 81·1 (63·5–77·0, M = 72·3) per cent of head.

Teeth. In fishes more than 50 mm S.L. the *outer row* of *premaxillary* teeth is composed of unequally bicuspid teeth anteriorly, but of tricuspids laterally and posteriorly (Text-fig. 8); the median cusp of the tricuspids, and the major cusp of the bicuspids is slightly incurved. Many specimens have some tricuspids intercalated amongst the biscuspids anteriorly, and in a few fishes almost the entire outer row is composed of tricuspid teeth. When there is a mixture of bi- and tricuspids the latter predominate. At all positions in the tooth row the bi- and tricuspids are of equal size.

Tooth morphology and arrangement in the *lower jaw* are similar to those in the upper, although more individuals have only tricuspid teeth present; a predominantly bicuspid outer row is rarely encountered.

Fishes in the size range 20–40 mm S.L. have mainly bicuspid teeth in the upper jaw, with those tricuspids present restricted to a posterolateral position in the row.

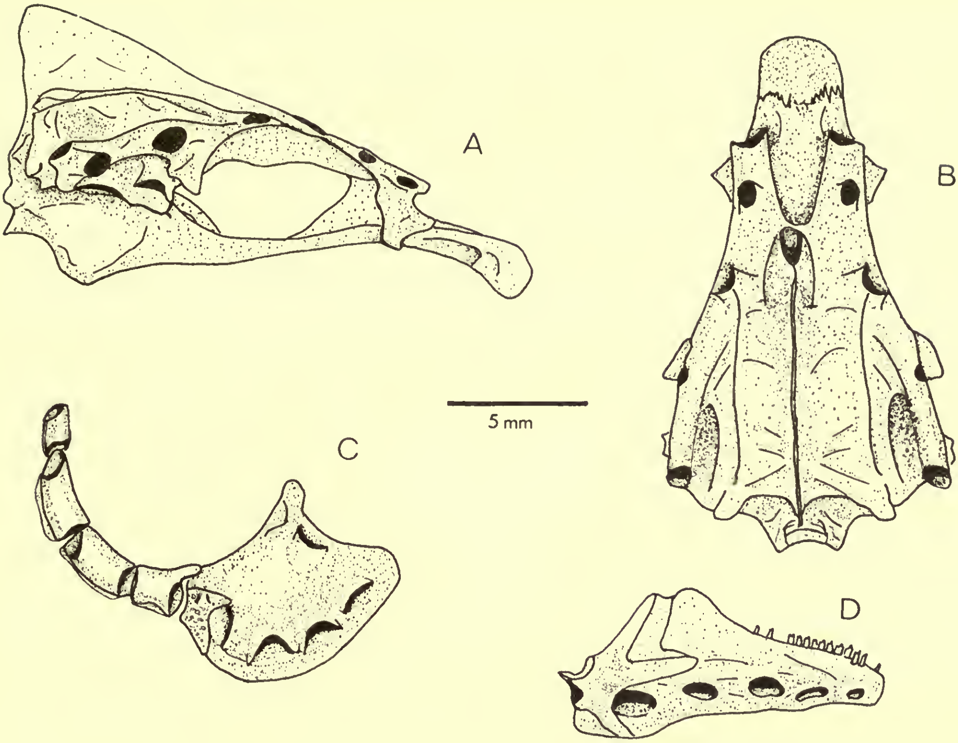

FIG. 9. *Haplochromis macconneli*. A : Neurocranium in right lateral view. B : Neurocranium, dorsal surface. C : Bones of the infraorbital series, right side. D : Right lower jaw, viewed from a slightly ventrolateral position.

Bicuspid teeth also predominate in the lower jaw, but some unicuspid (and slender) teeth may occur posterolaterally. Tooth form is like that of the larger fishes.

There are 41–64 (M = 52) outer premaxillary teeth in fishes 50–77 mm S.L., and 24–42 in specimens 22–39 mm long.

Irrespective of a fish's size, the *inner teeth* in both jaws are all tricuspid and small, and are usually arranged in a single series but double rows are encountered occasionally.

OSTEOLOGY. The characteristic hypertrophy in the cephalic laterosensory canal system has been commented upon above (*see also* Text-figs. 7 and 9). Canal bones in the pectoral skeleton are also affected, and the otic region of the skull is noticeably inflated (*see* Text-fig. 9).

The *neurocranium* (Text-fig. 9) departs from the generalized *Haplochromis* type (as seen in *H. rudolfianus*, Text-fig. 3) and clearly approaches that found in *H. saxicola* and allied species in the Lake Victoria species flock (Greenwood, 1974). In other words, the preotic region of the skull is slightly more elongate than in the generalized type, and associated with this and the shallower braincase, the preotic skull roof is straighter and slopes upwards at a smaller angle. The supraoccipital crest is lower than in most generalized types of skull, and the otic region is narrower.

Although all the canal bones of the skull (and also those bones encasing the inner ear) are noticeably inflated, the dermopterotics show the greatest hypertrophy of all (*see* Text-fig. 9A and B).

The *lower pharyngeal bone* (Text-fig. 10) is triangular in outline (length and breadth of the dentigerous surface almost equal), is relatively slender, and has an anterior blade that is neither noticeably long nor noticeably short. The teeth on this bone are rather sparsely arranged in 16–20 irregular rows. Without exception, the teeth are weakly bicuspid, with a low, blunt or even barely visible anterior cusp and a crown that slopes gently into the sharper and larger posterior cusp ; all are fine and compressed but those in the two median rows are somewhat coarser.

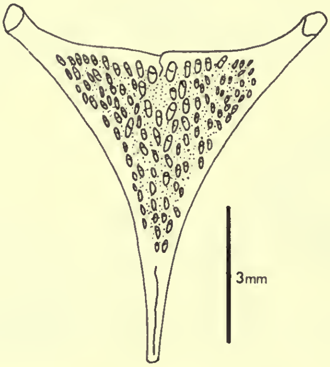

FIG. 10. *Haplochromis macconneli.* Lower pharyngeal bone in occlusal view.

Vertebrae and the caudal fin skeleton. Vertebral counts for the 24 specimens radiographed are : 27 (f1), 28 (f8), 29 (f14) or 30 (f1), comprising 12 (f16) or 13 (f8) abdominal and 15 (f1), 16 (f15) or 17 (f8) caudal centra. The fused first ural and first preural centra are excluded from these counts.

The caudal fin skeleton is unusual in showing a high degree of fusion between various hypurals (or if not fusion, such extremely close apposition as to be indistinguishable from fusion on radiographed specimens). The extent of fusion or apposition is generally complete, but in a few fishes there are short unfused sections between the otherwise conjoined elements.

About 77 per cent of the 26 specimens radiographed showed some degree of fusion between various hypurals. Only 6 specimens (*ca* 23 per cent of the sample) had all 5 hypurals completely free from each other. Most frequently (i.e. in 20 fishes) hypurals 1 and 2 are fused. In the upper part of the skeleton the commonest pattern of fusion is to have hypurals 3 and 4 fused, but hypural 5 free (11 specimens) ; only 4 specimens had all 3 upper hypurals fused, and 5 fishes showed no fusion between any of the 3 upper hypurals. In *H. rudolfianus*, it will be recalled, only 2 out of 30 specimens (i.e. about 7 per cent) had any fused hypurals ; in both these fishes fusion was between hypurals 1 and 2 (*see* p. 146).

For comparison with the situation in Lake Rudolf, the caudal skeleton in several endemic *Haplochromis* species from other lakes was examined. Of 174 specimens (representing 12 species) from Lake George, Uganda, about 8 per cent showed some (but never complete) fusion between elements in both the upper and the lower parts of the skeleton. The frequency of fusion seems equally distributed amongst the species examined.

In Lake Victoria, too, hypural fusion is relatively rare. One hundred and seventy-eight specimens representing 22 species (with a modal sample size of 10 specimens per species) were examined. Of these, 20 specimens (i.e. about 13 per cent) had fused hypurals. The commonest pattern here is of fusion between hypurals 3 and 4, less frequently it occurs between hypurals 1 and 2, and only once was it recorded, with certainty, between hypurals 1 and 2, and 3 and 4 in the same individual (although two other individuals may show this pattern). The Lake Victoria species examined are from several phyletic lineages within the *Haplochromis* flock of that lake and cover a wide range of body forms.

Far fewer specimens are available of the four endemic *Haplochromis* species from Lake Albert. Of these, *H. bullatus* Trewavas has 3 out of 18 fishes (i.e. about 17 per cent) with hypurals 1 and 2 fused (or very closely apposed), while *H. avium* Regan (9 specimens) and *H. albertianus* Regan (15 specimens) have none. Both the latter species, however, have some individuals in which the hypurals are closely apposed.

Thus, even allowing for the small sample sizes involved in this survey, it does seem that the frequency of hypural fusion in *H. macconneli* is exceptionally high. The significance of this phenomenon remains unexplained.

VISCERA. Because of poor preservation it is impossible to measure precisely the length of the gut in *H. macconneli*; I would estimate the intestine to be about $1\frac{1}{2}$ times longer than the standard length. In strong contrast to *H. rudolfianus* there is no trace of melanin in the peritoneal tissue and neither are the gonadial walls pigmented (*see* p. 146 above).

COLORATION. In life, *adult females* are a pale greenish-fawn with traces of greenish iridescence on the flanks. All fins are colourless except for three conspicuous and bright yellow spots on the anal.

Live colours for *males* have not been recorded.

Preserved colours. I suspect that the material I have examined is somewhat bleached and thus the coloration is probably lighter than it might otherwise have been.

There is apparently little sexual dichromatism. In both sexes the ground colour of the body and head is a pale yellowish-fawn with no tonal variation between dorsum and venter. All fins are hyaline with, in both sexes, dark maculations on the proximal third to half of the caudal fin. The males examined have the dorsal fin somewhat darker than that of the females, and there is a fairly dense aggregation of melanophores on the anterior third of the pelvic fins. (These specimens may, however, be less bleached than are the females.)

ECOLOGY. Judging from Mr Hopson's records, *H. macconneli* is confined to water more than 20 m deep, and is probably most abundant in deeper water (i.e. at depths of 50–70 m). Some of the smallest specimens collected (15–20 mm S.L.) were caught at a depth of 75 m, and none, of any size, has been recorded from littoral habitats. The pale coloration of this species and the absence of melanic pigments in the peritoneum and gonads may well be correlated with this deep-water distribution.

No data are available yet on the feeding habits of the species.

Breeding biology. The marked sexual dimorphism in adult size has been noted already (p. 154). Despite a very thorough search, Mr and Mrs Hopson were at first unable to find any males amongst the several hundreds of *H. macconneli* they examined. Eventually two males, 31·0 and 35·5 mm S.L., were identified in a catch made some 2·4 km east of North Island at a depth of 30 m. Both these fishes appear to be sexually adult ; one is probably in an advanced stage of ripening, the other at a slightly earlier stage of development. Females are certainly adult at a length of *ca* 50 mm and it seems likely that they may mature at a smaller size (Hopson *in litt.*). Be that as it may, females seem to grow to a much greater length than do males.

In a sample of 21 adult females examined, only 2 have both ovaries equally developed. Eleven fishes have the right ovary much larger than the left one (at all stages of oogenesis), and 8 have only the right ovary developed. Unlike *H. rudolfianus*, there is no trace of melanization in the ovarian wall of *H. macconneli*.

No details are available on the breeding habits or seasons of the species.

DIAGNOSIS AND AFFINITIES. *Haplochromis macconneli* is readily distinguished from the other Lake Rudolf species by the hypertrophy of its cephalic laterosensory canal system, its dentition (*see* p. 156), and in specimens > 35 mm S.L., from *H. rudolfianus* by several morphometric characters (deeper cheek and preorbital, longer snout, smaller eye and longer jaws).

Indeed, *H. macconneli* is so distinct morphologically from *H. rudolfianus* and *H. turkanae* (and the putative fourth species) that it is difficult to establish its phyletic affinities with these other taxa. In addition to the characters listed above, *H. macconneli* also differs from *H. rudolfianus* (and from the undescribed species too) in the shape of its neurocranium, which is of a more specialized type (*see above*, p. 157 and Greenwood, 1974). Almost certainly the hypertrophy of the cephalic lateral line canals is an adaptation associated with the deep-water habitat of *H. macconneli*, and strongly suggests that the species evolved within the lake. No fluviatile *Haplochromis* exhibits this specialization.

It is interesting to note that the cephalic lateral line canal hypertrophy seen in *H. macconneli* is much greater than that found in any known *Haplochromis* species living at comparable depths in Lake Victoria (Greenwood & Gee, 1969). Amongst *Haplochromis*-group species an equivalent hypertrophy is seen only in *H. bullatus* of Lake Albert, and in species of the endemic Lake Malawi genus *Trematocranus* (Trewavas, 1935). Species of another Malawi endemic, *Aulonocara*, show greater development in certain parts of the system (the infraorbital series for example), but otherwise exhibit a level of hypertrophy comparable with that of *H. macconneli*.

Trematocranus and *Aulonocara* are manifestly more closely related to each other and to other taxa from Lake Malawi (Trewavas, 1935 ; personal observations) than to any species occurring outside the lake. Neither need be considered further in the possible phylogeny of *H. macconneli.*

On purely morphological grounds *H. bullatus* of Lake Albert could be considered the nearest living relative of *H. macconneli.* Both species share the specialization of enlarged laterosensory canals on the head, and both share (with other species from Lakes Albert and Rudolf) certain peculiarities in the predorsal and thoracic squamation patterns (*see above*, p. 144). The latter character is, however, difficult to assess with respect to its being a primitive or a derived one. At present all that can be said is that the pattern is not encountered amongst the *Haplochromis* species of Lake Victoria nor is it seen in the fluviatile *Haplochromis* of Kenya, Uganda and Tanzania. It is rarely encountered in the *Haplochromis* species flock of Lakes Edward and George (where it is known from two species, *H. pharyngalis* Poll and *H. petronius* Greenwood ; *see* Greenwood, 1973), but it does seem to characterize the *Haplochromis* of the River Nile, Lake Albert, Lake Rudolf and the River Zaire (personal observations ; also Greenwood, 1971).

Haplochromis macconneli differs from *H. bullatus* in the shape of its neurocranium (*see* p. 157 above) which is like that found in the moderately specialized insectivore–piscivore radiation in Lake Victoria (*see* Greenwood, 1974, pp. 80–93). This difference would not, of course, debar *H. bullatus* from consideration as the living plesiomorph sister species of *H. macconneli.* But the fact that the Lake Rudolf and Lake Albert basins have never been interconnected (and if there had been some riverine connection, the probability that any presumed common ancestor of the two species would itself have been abyssal in habits) seems to rule out any such close phyletic relationship. Interspecific similarities in laterosensory canal hypertrophy are thus to be interpreted as the product of parallel evolution. The shared peculiarities in squamation patterns may well reflect a common ancestry but this is likely to be a relatively distant one (*see below*, p. 162).

It seems probable, therefore, that the relationships of *H. macconneli* should be sought amongst the species of Lake Rudolf. Two interpretations seem possible. First, *H. macconneli* may be an immediate derivative of an *H. rudolfianus*-like ancestor (i.e. *H. rudolfianus* and *H. macconneli* may be true sister species). Alternatively, *H. macconneli* might be the apomorph survivor of another lineage the relatively plesiomorph, that is *H. rudolfianus*-like members of which have become extinct (unlike the situation in Lake Victoria, for example, where it is possible to follow, from species still extant, the specialization of a lineage ; see Greenwood, 1974).

DISCUSSION

Even with the discovery of two and possibly three new *Haplochromis* species, the total fish fauna of Lake Rudolf still stands low on the scale of endemicity in African lakes. Its *Haplochromis* species flock also shows a low level of adaptive radiation, probably lower than that of Lake Albert (*see* Trewavas, 1938 ; Greenwood, 1971) where an anatomically specialized mollusc-eater, a specialized grazer on epiphytes and a species adapted for life in deep water have evolved.

This comparison must, however, be interpreted with care. For one thing, *H. mahagiensis* David & Poll (the mollusc-crushing species) of Lake Albert may well belong to a different lineage from that of the other species in the lake. It could be the local representative of a fluviatile mollusc-crushing species represented elsewhere by *H. straeleni* Poll and *H. vanderhorsti* Greenwood (*see* Greenwood, 1954 & 1959a, for discussion). Furthermore, a temporal element is probably involved. There is little evidence of Lake Albert having dried out at any time in its history, but Lake Rudolf probably was severely reduced, or even completely desiccated, during the middle part of the Pleistocene (*see* Fryer & Iles, 1972, for review). Refilling of the Rudolf basin appears to have been through what is now the River Sobat at some time within the later Pleistocene. Subsequently the connection was broken and has never been re-established. Such an historical background has two consequences, namely that Lake Rudolf is to be considered a relatively young lake, and that its colonizers (or, perhaps more accurately, its recolonizers) were species of Nilotic origin.

The relative youth of Lake Rudolf, coupled with the nature of its basin may, as Fryer & Iles (1972) suggest, account for the paucity of endemic species and, I would also suggest, for the muted adaptive radiation seen amongst the three or four *Haplochromis* species that evolved there.

With two exceptions, all the *Haplochromis* species of Lake Albert are apparently confined to the basin of that lake. The two more widely distributed species, *H. wingatii* (Blgr.) and *H. loati* Greenwood, both have dental specializations that are not shared with any Lake Rudolf taxa (Greenwood, 1971). Thus, it seems unlikely that an extant Albertine *Haplochromis* species was the original recolonizer of Lake Rudolf in later Pleistocene times. Nor does it seem probable that the recolonizer closely resembled any species from the Nile (amongst which must be considered *H. wingatii* and *H. loati* or their ancestors). In this situation the only conclusion that can be drawn is that some fluviatile species, now extinct, provided the founder population for the Lake Rudolf microflock.

It is, of course, possible that the present-day Rudolf species (or some part of them) are descendants from the relicts of a previous flock, possibly a more complex one, that inhabited the early Pleistocene lake and which survived the subsequent period of desiccation. The neurocranial differences between *H. rudolfianus* and *H. macconneli* might be explained in this way. If this was the history of the present-day species then it follows that their ancestors were derived not from the Nile (which did not then exist in its present form ; *see* Berry & Whiteman, 1968), but from a river that originated in the eastern highlands and emptied into the developing Nile system in the region of the present River Sobat.

Shared peculiarities in the squamation pattern of the thoracic and predorsal regions hint at a common ancestry for the Lake Rudolf and Lake Albert *Haplochromis* species (*see above*, p. 161). This character complex is not found in the *H. bloyeti*-like species group that is widespread in the rivers of Uganda, Kenya and Tanzania. Members of this species complex are thought to be close relatives of the ancestral species which gave rise to the sister species flocks in Lake Victoria and Lakes Edward and George (*see* Greenwood, 1973 & 1974). Fishes in these flocks, with one exception in Lake George and one in Lake Edward, all lack the Albert–Rudolf scale pattern. The exceptional species, *H. petronius* and *H. pharyngalis*, resemble the Nilotic *H. wingatii* in several features as well as the one of scale pattern, and they may represent an exotic element amongst the otherwise *H. bloyeti*-like derivatives inhabiting these lakes (Greenwood, 1974). The possible phyletic relationship of *Haplochromis* species from Lakes Rudolf and Albert raises some interesting points of zoogeography. The lakes are several hundred kilometres apart and any form of past interconnection they may have had would have been of an indirect nature (*see above*, p. 162). In contrast, Lake Albert is close to Lake Edward and the lakes are in direct contact through the River Semliki. Yet, their faunas, both cichlid and non-cichlid, are quite distinct (Greenwood, 1959b). The present barrier to faunal interchange, principally the Semliki rapids, is clearly an effective one.

I have argued elsewhere for a close phyletic relationship between the *Haplochromis* species of Lakes Edward and Victoria and for their derivation in parallel from a common ancestor that once inhabited the westward flowing rivers of eastern Africa during the Pleistocene (Greenwood, 1973). It seems now that perhaps this concept should be qualified by postulating an ancestral species that lived in some but not all of those rivers. The reasoning behind this qualification is, of course, the presence of species in Lake Albert that would seem to be derived from a different lineage, a lineage that also gave rise to the species of the Nile and, possibly, Lake Rudolf as well (*see above*, p. 161). Furthermore, it is possible that the *Haplochromis* species of the River Zaire may share ancestry with these species (p. 161).

The evidence upon which these postulated phylogenies are based, a shared scale pattern, is admittedly tenuous, particularly since it is not yet possible to determine which of the two types is to be considered the primitive condition. Further research is planned to investigate the phylogeny of *Haplochromis*-group species and I would certainly not consider the ideas expressed here as more than a working hypothesis.

The presence of two species with Albert–Rudolf scale patterns (*H. petronius* and *H. pharyngalis*) in Lakes George and Edward demands explanation. Three possible explanations can be considered. First, the ancestor of these species made its way into the Lake Edward basin in fairly recent times and *via* the River Semliki. The likelihood of this, however, is reduced by the fact that no reciprocal exchange of *Haplochromis* seems to have taken place (although the two lakes share another cichlid *Sarotherodon leucostictus* [Trewavas]). Second, the prerift rivers each may have contained species of both squamation types. The absence of species with the Albert–Rudolf pattern from most rivers in eastern Africa (and probably from Lake Victoria as well) would seem unlikely if both types had been represented there previously. The third possibility is one based on the assumption of there having been a single basin in which the proto-Lakes Albert and Edward developed, probably as a series of partly interconnected small and swampy lakes. The northern region of this basin (the future Lake Albert) could have been fed by rivers in which the *Haplochromis* species had an Albert–Rudolf facies, while the southern end (future Lakes Edward and George) was fed by rivers with *Haplochromis* of a Victoria–Edward facies. The next assumption would be that only a limited exchange of species took place between the two regions before their continuity was broken. Victoria-type species, if any penetrated to the north, were, presumably, unsuccessful in that environment or in competition with the Albert–Rudolf types. Such a general contact between the early lakes may also account for the similarity in their Pleistocene fish faunas (*see* Greenwood, 1959b ; also new and unpublished observations), although one can equally argue that a fauna of this type was widespread in the prerift river systems.

Whatever the explanation, it does seem that both Lake Albert and Lake Rudolf have, since their inceptions, been relatively isolated from each other and from other water bodies in eastern Africa.

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Pp. 167–188 ; 4 *Text-figures*

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A REVIEW OF *SCOTOECUS* THOMAS, 1901 (CHIROPTERA : VESPERTILIONIDAE)

By JOHN E. HILL

INTRODUCTION

CURRENT classification of the genus *Scotoecus* rests basically on Ellerman, Morrison-Scott & Hayman (1953 : 83) who recognized two species in southern Africa, one (*albofuscus*) with pale wings, the other (*hirundo*) with dark wings. Hayman (1963 : 104) expanded this opinion in a brief review, and allocated the named forms then in the genus to one or other of these as subspecies. Rosevear (1965 : 300) retained *falabae* from northern Nigeria as a distinct species, but Hayman & Hill (1971 : 36) recognized only *albofuscus* and *hirundo* as valid species. However, specimens examined recently at the British Museum (Natural History) have suggested that the dark-winged group is composed of two species, one smaller, for which *hirundo* is available, the other a little larger in size, for which the earliest name is *hindei*. Hitherto, *Scotoecus* has been considered exclusively African, but a study of the Indian species first described as *Scotophilus pallidus* by Dobson (1876 : 186) and nowadays generally referred to *Nycticeius* shows it to be more closely allied to *Scotoecus*, to which it is transferred.

Measurements throughout are in millimetres : minimum and maximum values are given for series, with (in parentheses) the number of specimens measured.

SYSTEMATIC SECTION

SCOTOECUS Thomas, 1901

Scotoecus Thomas, 1901 : 263. Type species *Scotophilus albofuscus* Thomas, 1890.

DIAGNOSIS. Similar to *Scotozous* and *Nycticeius* but with spatulate or nearly spatulate tragus (Fig. 1) ; braincase elevated frontally to give a slightly convex frontal profile ; rostrum greatly widened at the lachrymals ; narial and pre-palatal emarginations exceptionally deep ; zygomata tenuous, usually lost in preparation ; and anterior face of the upper canine flattened and grooved.

DESCRIPTION. Small (length of forearm 28–38) ; muzzle broad, flattened, anteriorly sparsely haired, nares circular, opening obliquely ; ear rounded with rounded tip, its anterior margin lacking any basal lobe ; tragus spatulate or nearly so with small, more or less triangular posterior basal lobe ; calcar extending along two thirds of the uropatagial margin with small post-calcarial lobe ; penis sometimes exceptionally long.

Skull low, braincase broad, with slight occipital helmet and low lambdoid and sagittal crests ; skull slightly elevated frontally to produce a faintly convex profile ; interorbital region wide, rostrum broad, much expanded at lachrymals ; anteorbital foramen moderate or large, closed by strong, nearly vertical bar ; small supra-orbital tubercles often present ; narial emargination wide, U-shaped or slightly

V-shaped, the apex rounded, deep, extending posteriorly at least to a line joining the anterior margins of the anteorbital foramina, sometimes to a line joining the anterior margins of the orbits ; pre-palatal emargination wide, extending posteriorly to a point lying between a line joining the anterior faces of the large upper premolars (pm^{4-4}) and a line joining the anterior faces of the first upper molars (m^{1-1}) ; zygomata tenuous, in African species often lost in preparation ; maxillary toothrows not markedly convergent anteriorly ; a narrow post-palatal spine and shallow basioccipital depressions.

Dental formula $i\frac{1}{3}$, $c\frac{1}{1}$, $pm\frac{2}{2}$, $m\frac{3}{3} = 32$ or $i\frac{1}{3}$, $c\frac{1}{1}$, $pm\frac{1}{2}$, $m\frac{3}{3} = 30$. Massive, unicuspid inner upper incisor (i^2), in contact with the canine or nearly so ; anterior face of upper canine flattened, grooved, sometimes prominently so ; anterior upper premolar (pm^2) minute or absent, when present compressed into a lingual recess between canine and the second upper premolar (pm^4) which are otherwise in contact ; pm^4 with antero-medial cusp or protocone low or absent ; upper molars (m^{1-3}) with protocones prominently developed ; the lingual shelves widely separated, m^3 not reduced, its crown area exceeding one half the crown area of m^1 or m^2, with prominent metacone, metastyle and three commissures ; lower incisors (i_{1-3}) imbricated ; anterior lower premolar in the Indian species reduced to one third to one half the crown area of the second lower premolar (pm_4) which is not compressed in the toothrow ; in the African species pm_2 a little less in crown area than pm_4, the latter slightly shortened antero-posteriorly, compressed between pm_2 and the first lower molar (m_1) ; third lower molar (m_3) not reduced or only very slightly reduced, its posterior triangle not at all or only a little smaller than the anterior triangle, hypoconid and entoconid present, the latter slightly the lesser.

LITERATURE. Trouessart, 1904 : 85 (spelt *Scotaecus*) ; Miller, 1907 : 217 (generic diagnosis) ; Wettstein, 1918 : 654 (review, key) ; Simpson, 1945 : 59 (incorporated into *Nycticeius*) ; Ellerman, Morrison-Scott & Hayman, 1953 : 83 (status, partial key, a subgenus of *Nycticeius*) ; Hayman, 1963 : 104 (review, tooth formula, variability of pm^2, a subgenus of *Nycticeius*) ; Koopman, 1965 : 17 (status, generically valid) ; Rosevear, 1965 : 289, 297 (status, description, partial key, generically valid) ; Ansell 1967 : 21 (as a genus) ; Hayman & Hill, 1971 : 36 (key, notes, distribution, subgenus of *Nycticeius*) ; Koopman, in litt., in Hayman & Hill, 1971 : 36 (a subgenus of *Nycticeius*).

DISTRIBUTION AND SPECIES. Indian and African, in India a semi-desert species inhabiting tropical thorn forest, in Africa occurring chiefly in open woodland in three species with few records from the high forest. The Indian species (first described as *Scotophilus pallidus* by Dobson, 1876 : 186) was for many years referred to *Scoteinus* (see below) but is here allocated to *Scotoecus* on account of its aural and rostral features, together with its grooved upper canines. Its features are less extreme than are those of the African species of *Scotoecus* and apparently it forms a link between these and *Nycticeius*, with which in recent years it has been associated The African members of the genus may be divided into two sections, the one pale-winged, with brownish ventral surface, the other dark-winged, the ventral surface pale, usually some shade of greyish. These correspond to the two species currently recognized in Africa by most modern authors. The examination of Ethiopian specimens and of specimens from Cameroon and Uganda in the course of preparing this study has suggested the further division of the dark-winged section into two species, one smaller, the other larger ; however, the genus is still known from relatively few specimens and the classification presented here is to that extent provisional. The species may be keyed :

1 Tragus long, relatively narrow ; zygomata not cartilaginous ; pm$_2$ reduced, its crown area one third to one half that of pm$_4$; this tooth not compressed in toothrow . . . . . . *pallidus* (p. 172)
– Tragus short, relatively wide ; zygomata cartilaginous ; pm$_2$ unreduced, its crown area subequal to that of pm$_4$; this tooth compressed in toothrow 2

2 Tragus more or less parallel-margined, the upper part of its anterior margin not prolonged anteriorly ; outer part of wing membrane pale ; ventral surface of body brown ; braincase slightly flattened *albofuscus* (p. 174)
– Tragus slightly hatchet-shaped, the upper part of its anterior margin projected forward ; outer part of wing membrane dark ; ventral surface of body greyish, at most tinged with brown ; braincase slightly elevated 3

3 Smaller, length of forearm generally less than 33·0, condylobasal length 13·2 or less, c–m^3 5·1 or less . . . . . . *hirundo* (p. 177)
– Larger, length of forearm generally exceeding 32·0, condylobasal length 13·5 or more, c–m^3 5·2 or more . . . . . . *hindei* (p. 179)

History. First separated from *Scotophilus* at the generic level by Thomas (1901 : 263), *Scotoecus* was considered generically valid by Miller (1907 : 217), who allied it with *Nycticeius* and *Scoteinus*. Allen (1939 : 98) listed *Scotoecus* as a distinct genus for Africa but since that date opinions of its status have diverged. Simpson (1945 : 59) incorporated it into *Nycticeius*, a lead followed by Ellerman, Morrison-Scott & Hayman (1963 : 83) who treated *Scotoecus* as a subgenus of *Nycticeius* with the comment that the characters given by Thomas and Miller seemed more subgeneric than generic. Hayman (1963 : 104) and Hayman & Hill (1971 : 36) adopted this view but Rosevear (1965 : 289) noted that *Scotoecus* is readily distinguished from *Nycticeius* and considered that it merited generic separation, a view followed by Ansell (1967 : 21) and shared by Koopman (1965 : 17) who did not consider *Scotoecus* congeneric with *Nycticeius* but later (in litt., in Hayman & Hill, 1971 : 36) revised this opinion to accord *Scotoecus* subgeneric rank only.

Remarks. There seem no good grounds for considering *Scotoecus* congeneric with *Nycticeius* : the form of the tragus, the elevated cranium and widened rostrum with deep anterior emarginations, and the grooved upper canines of *Scotoecus* separate it sharply from this genus. The convexity of the frontal area in *Scotoecus*, its broad rostrum with deep emarginations and its weak zygomata present a parallel with *Nyctalus*, in which, however, no modification of the upper incisors has occurred.

Scotoecus pallidus (Dobson, 1876)

? *Vespertilio noctulinus* Geoffroy, 1831 : 92, pl. 3. Bengal, India.
Scotophilus pallidus Dobson, 1876 : 186, Appendix D, 208. Mian Mir, Punjab, northwestern India.

DIAGNOSIS. Differing from the African *S. albofuscus*, *S. hirundo* and *S. hindei* in thicker, more fleshy ears, more swollen at the antitragus ; tragus (Fig. 1) longer and relatively narrower, its tip more expanded ; narial emargination faintly V-shaped, its lateral margins slightly convergent posteriorly, the apex rounded ; pre-palatal emargination narrower ; anteorbital foramen smaller ; zygomata tenuous but not cartilaginous ; anterior lower premolar (pm_2) reduced, its crown area one third to one half that of the second lower premolar (pm_4) which is not compressed in the toothrow ; third lower molar (m_3) slightly reduced, the posterior triangle a little narrower than the anterior triangle. Differs further from *S. hirundo* and *S. hindei* in less inflated and less elevated braincase, in this respect resembling *S. albofuscus*.

DESCRIPTION. Large for the genus (length of forearm 34–38) ; lips fleshy ; ear moderate, reaching about halfway to tip of muzzle, with fleshy membrane and antitragal thickening ; anterior margin of tragus straight, tip rounded, anteriorly directed, posterior margin convex, penis not exceptionally developed. Dorsal surface pale brown, tinged with fawn, ventral surface paler, greyish white.

Skull relatively massive, with (especially in older individuals) low occipital helmet and posterior sagittal and lambdoid crests ; slight supraorbital ridges with incipient supraorbital tubercles ; anterior margin of orbit nearly vertical, the supraorbital and lachrymal regions swollen ; anteorbital foramen moderate, closed by narrow bar ; narial emargination wide, faintly V-shaped, slightly narrowed posteriorly, its lateral margins slightly convergent, extending posteriorly a little more than halfway to the anterior orbital margin ; pre-palatal emargination wide, U-shaped, extending posteriorly to a line joining the anterior faces of the second upper premolars (pm^{4-4}) ; zygomata narrow, tenuous but not cartilaginous ; post-palatal extension narrow, with small, delicate post-palatal spine.

Dental formula $i\,\frac{1}{3}$, $c\,\frac{1}{1}$, $pm\,\frac{1}{2}$, $m\,\frac{3}{3} = 30$. Upper canine with flattened, faintly grooved anterior face ; small upper premolar (pm^2) absent ; large upper premolar (pm^4) compressed between the canine and the first upper molar (m^1), with small antero-medial cusp or protocone ; m^{1-3} with strong protocones, their lingual shelves widely separated ; anterior lower premolar (pm_2) much reduced, one third to one half the crown area of the second lower premolar (pm_4) and less than one half its height, compressed between the canine and pm_4 ; third lower molar (m_3) very slightly reduced, posterior triangle a little narrower than the anterior triangle, hypoconid and entoconid slightly smaller than protoconid, paraconid and metaconid.

MEASUREMENTS. Length of forearm (14) 34·1–38·4 ; condylobasal length (8) 14·1–14·9 ; condylocanine length (8) 13·9–14·7 ; least interorbital width (10) 4·0–4·4 ; zygomatic width (1) 10·5 ; width of braincase (9) 7·3–8·1 ; mastoid width (7) 8·9–9·7 ; c^1–c^1 (9) 4·9–5·5 ; m^3–m^3 (9) 6·5–6·9 ; c–m^3 (11) 5·2–5·7 ; c–m_3 (11) 5·8–6·2.

LITERATURE. Dobson, 1876 : 186 (description), 208 (holotype listed) ; 1878 : 257, 258 (in *Scoteinus*, a subgenus of *Scotophilus*), 264 (description repeated), pl. xv, fig. 3 (ear) ; Blanford, 1891 : 222 (further description) ; Trouessart, 1897 : 119, 1904 : 85 (in *Scoteinus*, a subgenus of *Scotophilus*) ; Siddiqi, 1961 : 125 (Pakistan localities reviewed) ; Sinha & Chakraborty, 1971 : 53 (cranial features, measurements), figs. 1A, 2A, 3A (skull).

DISTRIBUTION. WEST PAKISTAN (Sind : Dobson, 1877 : 310 ; Anderson, 1881 : 137 ; Wroughton, 1916 : 752 ; Siddiqi, 1961 : 125 ; Sinha & Chakraborty, 1971 : 54). INDIA (Punjab : Dobson, 1876 : 186, 208, 1877 : 310, 1878 : 264 ; Anderson, 1881 : 137 ; Allen, 1908 : 48. Uttar Pradesh ; Bihar : Khajuria, 1951 : 120 ; Sinha & Chakraborty, 1971 : 54 ; specimens collected at Bahgownie, Darbhanga District, Bihar by N. A. Baptista in the collections of the British Museum (Natural History)). The record from Massowa, Eritrea, Ethiopia by Thomas & Doria (1886 : 206) in fact refers to *Nycticeius schlieffenii*, these authors having been misled by a comparison with a specimen of *schlieffenii* with an erroneous locality, identified by Dobson as *pallidus* (Thomas, 1890 : 86).

HISTORY. A rarely collected species to which there are relatively few references. Described as a *Scotophilus*, the species was placed by Dobson (1878 : 257, 258) and by Trouessart (1897 : 119, 1904 : 85) in the subgenus *Scoteinus*, subsequently elevated to generic rank by Miller (1907 : 217) but diagnosed by this author without reference either to its type species (designated by Miller, p. 217) *Scotophilus emarginatus* Dobson, 1871 or to *Scotophilus pallidus* Dobson, 1876. The type species has been shown by Sinha & Chakraborty (1971 : 53) to be congeneric with the species known for many years as *Scotomanes ornatus* (Blyth, 1851)* and *pallidus* does not in any event conform to the diagnosis of *Scoteinus* by Miller : the lachrymal region is widened as in the African species of *Scotoecus* and the third molars (m $\frac{3}{3}$) are almost unreduced, the narrowing of the rostrum and reduction of m $\frac{3}{3}$ being the chief diagnostic features of *Scoteinus* as understood by Miller, who had seen only the Australian species *balstoni* and *greyii* and the African *schlieffenii*, all nowadays usually referred to *Nycticeius*.

REMARKS. As might be expected from the disjunct distribution, the Indian *S. pallidus* differs more widely from its African congeners than these do from each other. In particular, a number of its features are less extreme than in the African species and its dentition approaches more nearly to the type exemplified by *Nycticeius*. There seem no good grounds for referring *pallidus* to this genus, however, since in *Nycticeius* the rostrum is not broadened and the upper canine is rounded anteriorly, not at all flattened or grooved : the same is true of the Australian species referred hitherto to *Scoteinus* and more recently to *Nycticeius*. In these, additionally, a greater measure of reduction of the third molars (m $\frac{3}{3}$) has occurred.

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* The generic synonymy was not discussed by Sinha and Chakraborty. *Scoteinus* and *Scotomanes* were proposed simultaneously by Dobson (1875: 371) *Scoteinus* having line priority. Article 24 of the International Code of Zoological Nomenclature provides that in such a case the relative priority of the names is determined by the action of the first reviser. Sinha and Chakraborty may be considered to be first revisers and continue to use *Scotomanes*. In view of the varied uses of *Scoteinus* this action is in accord with Recommendation 24A of the International Code, which suggests that the name that ensures stability and universality of nomenclature be selected.

Vespertilio noctulinus I. Geoffroy, 1831. Tate (1942 : 282) and Ellerman & Morrison-Scott (1951 : 177) suggested that this name should be associated with *pallidus* rather than considered a synonym of *Scotophilus temminckii* (= *S. kuhlii*) as it had been hitherto. It has a long history in the early literature : the description is repeated by Temminck (1840 : 211), who, in a supplement to the same work, subsequently provided (p. 266) a further description with details of the dentition, referring specimens from Singapore in the collections of the Rijksmuseum van Natuurlijke Historie, Leiden, to *noctulinus*. Cantor (1846 : 185), in a catalogue of the mammals of the Malay Peninsula referred the name to the synonymy of *Scotophilus temminckii* (= *S. kuhlii*) with the comment that *Nycticeius noctulinus*, Temminck referred to the young of the species, a view supported by Jentink (1888 : 183) who listed a young example of '*Vespertilio noctulinus* Is. Geoffroy' as *Scotophilus temminckii*. Wagner (1840 : 543, 1855 : 765) also provided further descriptions : Fitzinger (1870 : 367) gave a detailed synonymy to that date, with another description (as *Nycticejus noctulinus*) but Dobson (1876 : 120, 1878 : 258) referred the name to the synonymy of *Scotophilus temminckii*. Here it has since remained (Blanford, 1891 : 320, although this author evidently had some reservations, placing a query after the allocation ; Trouessart, 1897 : 118) until recent years. It is of interest to note that Oldfield Thomas has made a marginal note in his copy of Dobson's Catalogue (1878) which reads 'Size of a pipistrelle! F.a. 36 (Not a *Scotophilus*)!' – the grounds on which Tate suggested association with *pallidus*.

Scotoecus albofuscus (Thomas, 1890)

DIAGNOSIS. Similar to *S. pallidus* but smaller ; ears not especially fleshy ; tragus (Fig. 1) smaller, spatulate, not prolonged anteriorly ; distal part of wing whitish ; supraorbital region widely expanded ; lateral margins of narial emargination not convergent posteriorly ; anteorbital foramen large ; zygomata cartilaginous ; anterior lower premolar (pm_2) unreduced and third lower molar (m_3) barely reduced.

DESCRIPTION. Small (length of forearm 28·5–31·0) ; ear membrane and antitragus relatively thin ; tragus small, spatulate, upper part of its anterior margin not prolonged anteriorly. Dorsal surface brown, ventral surface similar but slightly paler ; wing blackish brown from body to a line joining elbow to knee but whitish from forearm, the forearm and digits dark ; interfemoral membrane dark brown.

Skull with broad, low, flattened braincase ; supraorbital region widely expanded ; narial emargination U-shaped, its lateral margins not convergent posteriorly ; anteorbital foramen large, closed by a strong, nearly vertical bar ; zygomata cartilaginous, often lost in preparation.

Dental formula $i\,\frac{1}{3}$, $c\,\frac{1}{1}$, $pm\,\frac{1}{2}$, $m\,\frac{3}{3} = 30$. Upper canine with flattened, strongly grooved anterior face ; small upper premolar (pm^2) absent in all eight specimens examined and in one (No. 22412, Musée Royale d'Afrique Centrale, Tervuren) seen by Dr F. de Vree (in litt.) ; large upper premolar (pm^4) with antero-medial cusp or

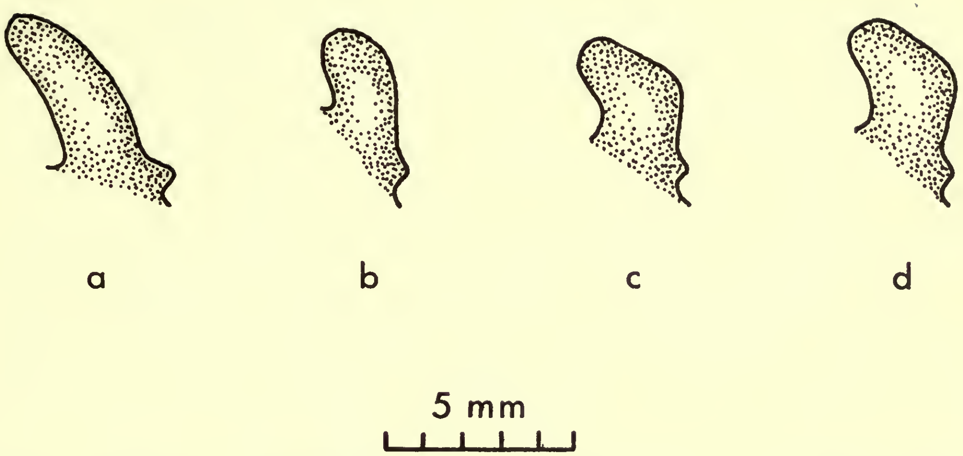

FIG. 1. Tragus of (a) *Scotoecus pallidus*. (b) *Scotoecus albofuscus*. (c) *Scotoecus hirundo*. (d) *Scotoecus hindei*.

protocone low or absent ; upper molars (m^{1-3}) with strongly developed protocones ; anterior lower premolar (pm_2) unreduced, its crown area almost equal to that of the second lower premolar (pm_4) which is compressed in the toothrow and is slightly flattened antero-posteriorly ; third lower molar (m_3) barely reduced, the width of its posterior triangle nearly equal to that of the anterior triangle.

DISTRIBUTION AND SUBSPECIES. Known from a limited number of specimens from localities in West Africa, Zaire, Tanzania and Malawi. Following Hayman (1963 : 105), Hayman & Hill (1971 : 37) recognized three subspecies, *S. a. albofuscus* in West Africa, *S. a. cinnamomeus* Wettstein, 1916 in the Sudan and *S. a. woodi* Thomas, 1917 in southern and eastern Zaire, Tanzania and Malawi. However, *cinnamomeus* is based upon an example of *Nycticeius schlieffenii**.

Scotoecus albofuscus albofuscus (Thomas, 1890)

Scotophilus albofuscus Thomas, 1890 : 84. Bathurst, Gambia.

DIAGNOSIS. Upper canine with rounded base, its antero-internal margin not sharply angular, postero-internal margin rounded, lingual shelf narrow.

MEASUREMENTS. Length of forearm (4) 29·8–31·0 ; condylobasal length (3) 12·7–13·5 ; condylocanine length (3) 12·8–13·3 ; least interorbital width (3) 4·1–4·4 ; zygomatic width — ; width of braincase (4) 7·3–7·7 ; mastoid width (3) 8·2–9·0 ; c^1–c^1 (3) 4·4–5·1 ; m^3–m^3 (3) 6·6–6·7 ; c–m^3 (4) 4·7–5·0 ; c–m_3 (2) 5·1–5·3.

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* The status of *cinnamomeus* Wettstein, 1916 from Kordofan has been reviewed in some detail by Kock (1969: 188). The preliminary description by Wettstein (1916: 191) was succeeded by a more detailed study (1918: 653) with illustrations (p. 653, fig. 12) of the ear and tragus and more particularly (pl. 4, figs. 5, 5a-b) of the skull and dentition. As Kock points out, these ally *cinnamomeus* undoubtedly with *Nycticeius schlieffenii*. This opinion is supported by Koopman (in litt., in Hayman & Hill, 1971: 37) who has examined the holotype in Vienna.

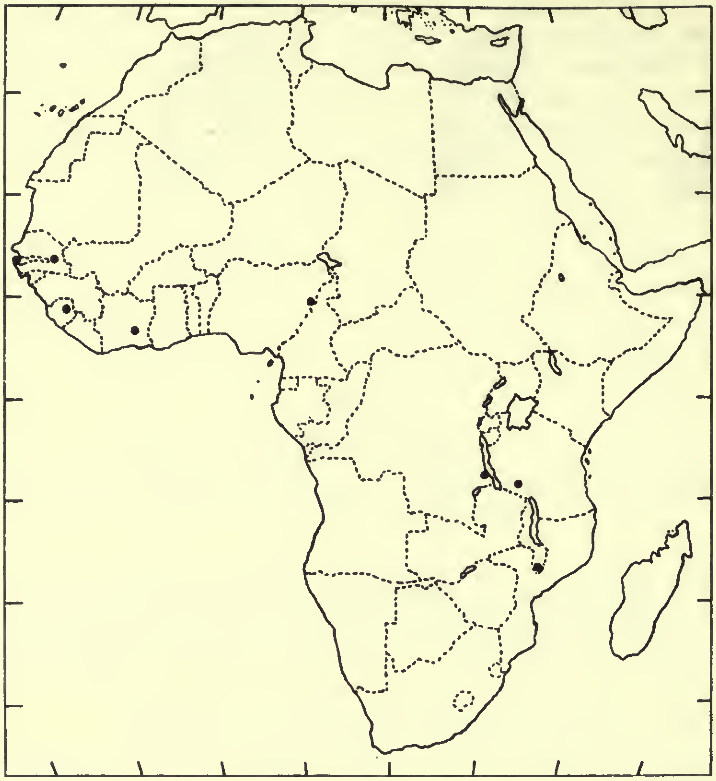

FIG. 2. Distribution of *Scotoecus albofuscus*.

LITERATURE. Rosevear, 1965 : 298, 299 (description), fig. 78 (skull), 305, fig. 80a (tragus).

DISTRIBUTION. SENEGAL (Badi : Thomas, 1911 : 119, as a location in Gambia) ; GAMBIA ; SIERRA LEONE (both Rosevear, 1965 : 299, from specimens in British Museum (Natural History)) ; IVORY COAST (Ayérémou (= Ahiérémou, 6°14′ N., 4°56′ W. ?), specimens in the Muséum d'Histoire Naturelle, Geneva (F. de Vree, in litt.)) ; NIGERIA (Dollman, 1908 : 546).

Scotoecus albofuscus woodi Thomas, 1917

Scotoecus woodi Thomas, 1917 : 280. Chiromo, southern Malawi, 200 feet.

DIAGNOSIS. Upper canine with angular base, its antero-lateral margin forming a right angle, postero-internal margin angular and projecting, the lingual shelf wide.

MEASUREMENTS. Length of forearm (5) 28·5–30·5 ; condylobasal length (4) 12·9–13·7 ; condylocanine length (4) 12·9–13·7 ; least interorbital width (4) 4·1–4·3 ; zygomatic width — ; width of braincase (4) 7·2–7·6 ; mastoid width (3) 8·8–9·0 ;

c^1–c^1 (4) 4·8–5·1 ; m^3–m^3 (4) 6·3–6·8 ; c–m^3 (4) 4·8–5·1 ; c–m_3 (4) 5·1–5·5 (specimens all from Chiromo, Malawi). Dr F. de Vree (in litt.) has measured a specimen (No. 22412) in the Musée Royale d'Afrique Centrale, Tervuren, from Baudouinville (07°03′ S., 29°42′ E.), Zaire : length of forearm 29·4 ; condylobasal length 12·9 ; least interorbital width 4·6 ; zygomatic width — ; width of braincase 7·3 ; mastoid width c. 8·4 ; m^3–m^3 6·7 ; c–m^3 5·2 ; c–m^3 (alveoli) 4·8 ; c–m_3 (alveoli) 5·5.

LITERATURE. Harrison, 1958 : 98, fig. 1 (whole animal), fig. 2 (head).

DISTRIBUTION. ZAIRE (Hayman, 1957 : 44 ; Hayman, Misonne & Verheyen, 1966 : 56) ; TANZANIA (Harrison, 1958 : 96 ; Vesey-Fitzgerald, 1964 : 64) ; MALAWI ; probably in ZAMBIA (Ansell, 1960, Appendix A, p. 110, Appendix B, p. 117).

REMARKS. According to Thomas (1917 : 280), *woodi* of southern Africa can be distinguished from the West African *albofuscus* by its smaller size, proportionately broader skull and by the different shape of the base of the upper canine. The small series of *albofuscus* and *woodi* available in the collections of the British Museum (Natural History) do not support the statement that *woodi* is significantly smaller than *albofuscus* and it appears to differ in size from *albofuscus* only in a generally very slightly wider rostrum, equalled in width by one of *albofuscus*.

Scotoecus hirundo (de Winton, 1899)

Scotophilus hirundo de Winton, 1899 : 355. Gambaja, Ghana, 1300 feet.

DIAGNOSIS. Similar in most respects to *S. albofuscus* but anterior margin of tragus (Fig. 1) projected anteriorly in its distal part to give the tragus a slightly hatchet-shaped outline, its upper margin nearly horizontal, the junction of the upper and posterior margins angular, slightly obtuse ; wing membranes wholly dark ; ventral surface of body some shade of grey ; braincase slightly inflated and rounded dorsally, less flattened ; pm^2 usually but not always present, the dental formula

$i\,\frac{1}{3}$, $c\,\frac{1}{1}$, $pm\,\frac{2}{2}$, $m\,\frac{3}{3} = 32$ or $i\,\frac{1}{1}$, $c\,\frac{1}{1}$, $pm\,\frac{1}{2}$, $m\,\frac{3}{3} = 30$.

VARIABILITY OF PM^2. The presence of a minute anterior upper premolar (pm^2) sandwiched tightly between the canine and pm^4 is variable in *S. hirundo*, pm^2 being totally absent from three of the nineteen specimens examined. The tooth is present in both sides of the jaw in a specimen (in the Muséum National d'Histoire Naturelle, Paris) from Saboya, Senegal. Dr F. de Vree (in litt.) has examined further specimens (in the Muséum d'Histoire Naturelle, Geneva) from the Bandia Forest, Senegal : two of these possessed the small pm^2 but so far as could be seen, this was lacking from a third. It is present in both sides of the jaw in one from Sierra Leone but totally absent from another (Hayman, 1963 : 105). There is no trace of pm^2 in the holotype from Ghana : it is present on both sides of the jaw in one specimen from the Cameroon but in another present in the left hand side only. Of ten examples from Ethiopia, eight have the tooth on both sides of the jaw, in one it is present in the right hand side only and in one it is totally absent. Three specimens from Uganda have pm^2 present on both sides of the jaw.

Measurements. Length of forearm (18) 29·7–32·8 ; greatest length of skull (15) 12·6–13·7 ; condylobasal length (16) 12·1–13·0 ; condylocanine length (16) 12·1–13·1 ; width of rostrum (18) 5·9–6·5 ; width across anteorbital foramina (18) 4·6–5·2 ; least interorbital width (18) 4·2–4·6 ; zygomatic width (1) 10·3 ; width of braincase (16) 7·0–7·7 ; mastoid width (13) 8·0–8·8 ; c^1–c^1 (18) 4·3–5·0 ; m^3–m^3 (18) 5·9–6·7 ; c–m^3 (18) 4·7–5·1 ; length of complete mandible (15) 8·9–9·9 ; c–m_3 (18) 4·9–5·4. Dr F. de Vree (in litt.) has measured three specimens (see above) (one skull only prepared) from the Bandia Forest, Senegal : length of forearm 31·0–32·3 ; greatest length of skull 13·9 ; condylobasal length 12·9 ; least interorbital width 4·7 ; width of braincase 7·8 ; mastoid width 8·9 ; m^3–m^3 6·5 ; c–m^3 5·3 ; c–m^3 (alveoli) 4·9 ; length of mandible 10·1, c–m_3 (alveoli) 5·3.

Literature. Rosevear, 1965 : 300 (further description), 305, fig. 80c (tragus).

Distribution. Senegal (Saboya, specimen in Muséum National d'Histoire Naturelle, Paris ; Bandia Forest, specimens in the Muséum d'Histoire Naturelle, Geneva (F. de Vree, in litt.)) ; Sierra Leone (Hayman, 1963 : 105) ; Ghana ; Cameroon (Yagoua, specimens obtained by F. de Vree and W. Verheyen) ; Ethiopia (Gambela, 515 and 1768 metres, 8°15′ N., 34°35′ E., and Didessa River, Wollega Province, 1190 metres, 9°02′ N., 36°09′ E., specimens in British Museum (Natural History)); Uganda (Budongo, 1°39′ N., 31°35′ E., specimens in British Museum (Natural History)).

Remarks. In recent years (following Hayman, 1963 : 104) the named forms in the dark-winged section of *Scotoecus* have been considered subspecies of *hirundo*, the earliest name. However, measurements of specimens in the collections of the British Museum (Natural History) and of specimens examined in 1971 for Dr F. de Vree, Antwerp, suggest that two species are involved, basically one of smaller size and northern distribution for which the prior name is *hirundo*, and a second species of larger size and predominantly more southern distribution for which the earliest name is *hindei*.

A specimen (B.M. 72.4421) from the Didessa River, Wollega Province, Ethiopia, is in close agreement with *hirundo* from West Africa : another (B.M. 72.4423) from the same locality is clearly referable to *hindei*. These are supported by a series of specimens (B.M. 70.2263–2270) and a further example (B.M. 72.4420), all from Gambela, western Ethiopia, which agree with *hirundo* : others (B.M. 70.2262, 72.4422) from Bulcha, Lake Margherita, some 200 miles to the southeast of Gambela, are referable to *hindei*. *Scotoecus* has apparently not been collected hitherto in Ethiopia. The two also occur almost sympatrically in Uganda : specimens (B.M. 74.1–5) (including pregnant or lactating females) obtained at Budongo (1°39′ N., 31°35′ E.) by J. F. Kingdon and clearly referable to *hirundo* contrast sharply in size with others (B.M. 63.1151, 65.3435) referable to *hindei* from West Madi (3°30′ N., 31°35′ E.) and Nabumali, South Bugisu (0°59′ N., 34°12′ E.). Furthermore, two specimens obtained at Yagoua, northern Cameroon, by F. de Vree and W. Verheyen agree very closely with *hirundo* and were collected concurrently at that locality with two further larger specimens referable with little doubt to *falabae*, here considered to be a subspecies of *hindei*. No *Scotoecus* has been reported hitherto from the

Cameroon. There is evidence to suggest, therefore, that in Ethiopia a small species (*hirundo*) occurs with or in close proximity to a larger species (*hindei*) : both occur in nearby localities in Uganda and are again sympatric in the Cameroon. Measurements of *hirundo* and of *hindei* from the areas of sympatry or near sympatry are contrasted in Table 1.

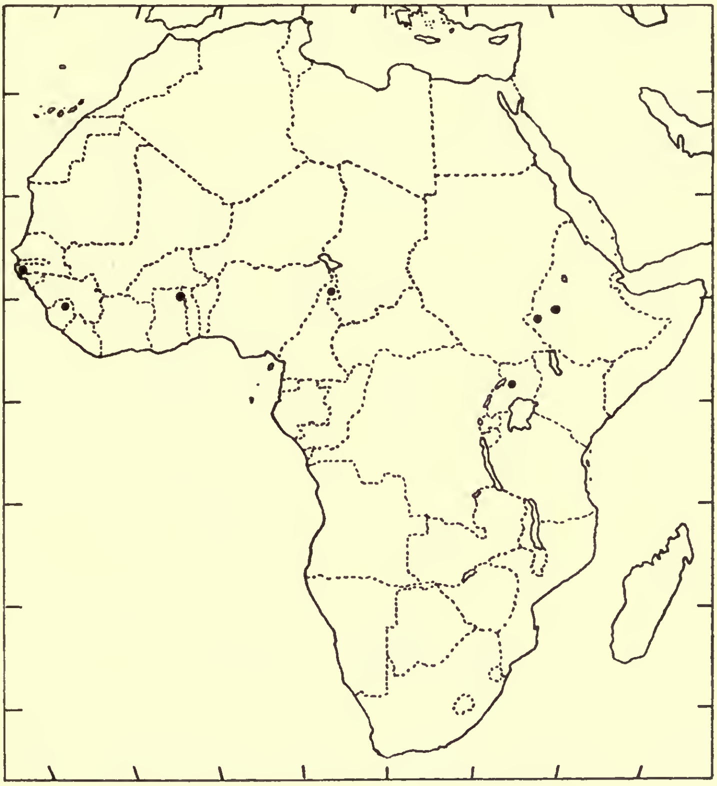

FIG. 3. Distribution of *Scotoecus hirundo.*

Scotoecus hindei Thomas, 1901

DIAGNOSIS. Similar to *S. hirundo* but larger, especially cranially, with the supraorbital and anteorbital regions wider and more greatly expanded.

VARIABILITY OF PM². The minute anterior upper premolar (pm²) is generally present in *S. hindei* : its presence in twenty-six examples in the collection of the British Museum (Natural History) is variable only in those from Ethiopia and Kenya. The tooth is present on both sides of the jaw in two specimens from Ethiopia, but in a third example present only in the left-hand side of the jaw. Among Kenyan specimens, the tooth is present on both sides in eight, present in the right-hand side but absent from the left in another, and totally absent from two further examples, one the holotype of *S. hindei hindei*. Hollister (1918 : 94) notes that pm² is completely absent from one of five Kenyan specimens in the Museum of Natural History,

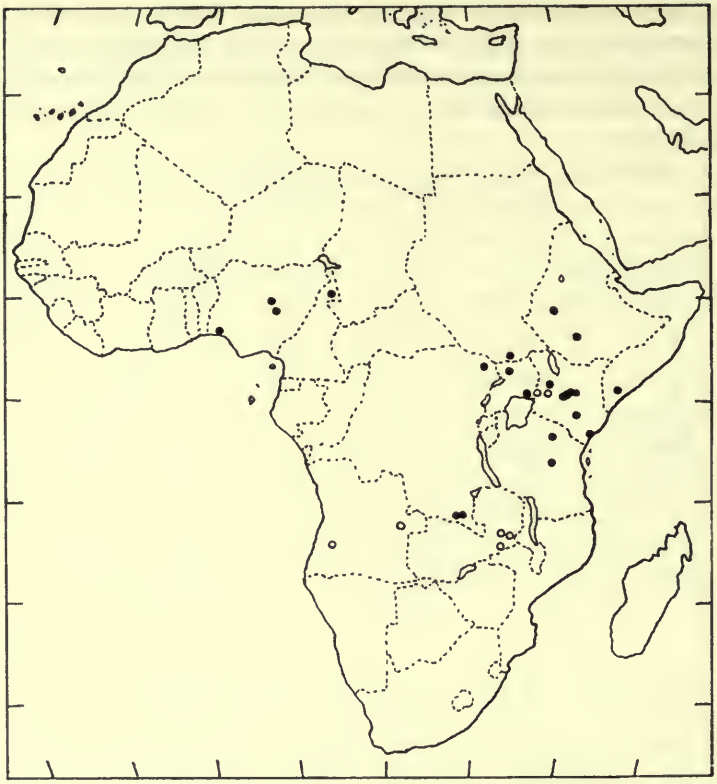

FIG. 4. Distribution of *Scotoecus hindei*. Records referred to *S. h. albigula* are indicated by unshaded circles ○.

the Smithsonian Institution, Washington, but that an alveolus can be seen on one side. The tooth is present in a further specimen reported (as *albigula*) by this author from Kiriba, Sudan (see below). Furthermore, Dr F. de Vree notes (in litt.) that pm^2 is absent from a specimen (M.R.A.C. 22192) in the Musée Royale d'Afrique Centrale, Tervuren, from Kapalowe, Katanga Zaire. Allen (1911 : 330) describes pm^2 in detail.

DISTRIBUTION. Nigeria, Cameroon and Sudan to Ethiopia and Somalia ; Kenya, Uganda and Tanzania to Zambia ; Zaire ; Angola.

Scotoecus hindei hindei Thomas, 1901

Scotoecus hindei Thomas, 1901 : 264. Kitui, Kenya, 1150 metres (in original description as 3500 feet).

(?) *Scotoecus artinii* de Beaux, 1923 : 98. Archer's Post, northern Guaso Nyiro, Kenya.

MEASUREMENTS. Length of forearm (15) 32·0–37·2 ; greatest length of skull (14) 13·8–15·0 : condylobasal length (15) 13·4–14·4 ; condylocanine length (15) 13·3–14·4 ; width of rostrum (14) 6·6–7·8 ; width across anteorbital foramina (14)

5·1–6·0 ; least interorbital width (15) 4·4–4·8 ; zygomatic width (1) 10·7 ; width of braincase (15) 7·3–8·0 ; mastoid width (15) 8·8–9·7 ; c^1–c^1 (14) 5·0–5·6 ; m^3–m^3 (14) 6·6–7·4 ; c–m^3 (16) 5·3–5·7 ; length of complete mandible (13) 10·0–11·2 ; c–m_3 (16) 5·5–6·4. Dr F. de Vree (in litt.) has measured a specimen (see above) from Kapalowe, Katanga, Zaire : length of forearm 33·2 ; greatest length of skull 14·7 ; condylobasal length 13·8 ; least interorbital width 4·5 ; zygomatic width 10·5 ; width of braincase 7·6 ; mastoid width 9·1 ; m^3–m^3 7·0 ; c–m^3 5·4 ; c–m^3 (alveoli) 4·9 ; length of mandible 10·1 ; c–m_3 (alveoli) 5·3.

DISTRIBUTION. SUDAN (G. M. Allen, 1914 : 349, as *Scoteinus schlieffenii*, identified as *Scotoecus* by Koopman, 1965 : 16 ; Hollister, 1918 : 94, from Kiriba, 'Uganda', a locality in southern Sudan according to Kock, 1969 : 192, as *albigula* ; Kock, 1969 : 192) ; ETHIOPIA (from Bulcha, Lake Margherita, 1800 metres, 6°11′ N., 38°10′ E., and from Didessa River, Wollega Province, 1190 metres, 9°02′ N., 36°09′ E., specimens in British Museum (Natural History)) ; SOMALIA (de Beaux, 1924 : 155, as *artinii* ; Funaioli, 1971 : 29, 64, as *hirundo*) ; ZAIRE (J. A. Allen, 1916 : 447, as *Scoteinus schlieffenii*, identified as *Scotoecus hirundo hindei* by Koopman, 1965 : 16 ; Hayman, 1954 : 291 ; Leleup, 1956 : 77 ; Anciaux de Faveaux, 1958 : 271 ; Hayman, Misonne & Verheyen, 1966 : 56) ; UGANDA (Hayman & Hill, 1971 ; 36, as *albigula*) ; KENYA (G. M. Allen, 1911 : 330 ; Dollman, 1914 : 309, in part Nos. 148, 149, 150, as *Scoteinus schlieffenii*, re-identified in the present study ; Hollister, 1918 : 94 ; Harrison, 1961 : 293) ; TANZANIA (a manuscript note by R. W. Hayman in a British Museum (Natural History) copy of Hayman & Swynnerton, 1951 (p. 294), records a specimen from Lake Mangona, but this example not seen ; Dodoma, specimen in British Museum (Natural History)).

Scotoecus artinii de Beaux, 1923. The precise status of *artinii* is far from clear. Koopman (1965 : 17) is inclined to regard *artinii*, *hindei* and a third more southerly form, *albigula*, as synonymous and notes that a specimen reported from Niangara, eastern Zaire, by J. A. Allen (1916 : 447) as *Scoteinus schlieffenii* is in fact a *Scotoecus*, referring it to *S. hirundo hindei* (= *S. hindei hindei*) with the remark that its best agreement seems to be with *artinii*. Hayman & Hill (1971 : 36) listed *artinii* as a subspecies of *hirundo* (*S. hindei* as here understood), considering (p. 37) on the basis of specimens from the Cherangani Hills, western Kenya, that possibly it might be a small form distinct from both *hindei* and *albigula*.

Three specimens attributed to *artinii* by R. W. Hayman were collected in 1966 by Mr A. N. Start at the Wei Wei River, Sigor, northeastern Cherangani Hills, Kenya, at about 3000 feet, the same collector subsequently obtaining in 1967 further examples (now B.M. 68.481–482) at the same locality. Mr Start also obtained three specimens attributed to *albigula* by R. W. Hayman from the Cherangani Hills at 6000 feet in 1965. Of these eight it has been possible to examine only B.M. 68.481–482, but the collections of the British Museum (Natural History) include three further examples (B.M. 14.7.31.15–17) of *S. hindei* from the Wei Wei River, formerly identified as *Scoteinus schlieffenii* (Nos. 148, 149, 150 of Dollman, 1914 : 309).

Male specimens from the Wei Wei River agree quite closely with the male holotype of *S. hindei hindei* and with male specimens referred to this subspecies from the

Lorian Swamp and the Guaso Nyiro, differing only in their slightly more slender canines. In this respect they resemble the male examples B.M. 63.1151 from West Madi, Uganda, and B.M. 65.3435 from Nabumali, South Bugisu, Uganda. However, a single male specimen collected 30 miles northwest of Baringo, Kenya, bridges this difference. Specimens from the Wei Wei River and from Uganda are generally a little smaller than specimens from more easterly locations and are similar in size to the specimen from Zaire measured by J. A. Allen (1916 : 447) (as *Scoteinus schlieffenii*). On the whole they are a little larger than specimens of *S. hindei* from the northern Cameroon.

De Beaux gives few diagnostic characters for *artinii* but his measurements indicate a short skull with the palatal width and toothrow dimensions of *S. hindei* : Hollister (1918 : 94) reports *hindei* from Archer's Post, Kenya, the type locality of *artinii*. For the present *artinii* is considered a provisional synonym of *S. h. hindei* but there remains the possibility that a subspecies with slender canines is to be found in western Kenya, Uganda and eastern Zaire and it is to this that perhaps *artinii* refers. If *artinii* can be distinguished then three subspecies of *hindei* occur in Kenya, namely *S. h. hindei* to the north, east and south, *S. h. artinii* to the west and northwest and *S. h. albigula* to the southwest. It is possible also that the rather larger *albigula* may be found to be specifically valid, but direct sympatry with *hindei* (including *artinii*) has yet to be demonstrated. The reported occurrences of the three forms in East Africa display a degree of overlap.

Scotoecus hindei albigula Thomas, 1909

Scotoecus albigula Thomas, 1909 : 544. Kirui, Mount Elgon, Kenya, 6000 feet.

DIAGNOSTIC. Larger than *S. h. hindei*, with larger, more massive teeth ; canines longer and heavier.

MEASUREMENTS. Length of forearm (3) 35·0–38·5 ; greatest length of skull (3) 15·3–15·5 ; condylobasal length (3) 14·7–14·8 ; condylocanine length (3) 14·8–15·0 ; width of rostrum (3) 7·2–7·7 ; width across anteorbital foramina (3) 5·7–6·0 ; least interorbital width (3) 4·5–4·9 ; zygomatic width — ; width of braincase (3) 8·0–8·1 ; mastoid width (3) 9·6–9·9 ; c^1–c^1 5·3–5·8 ; m^3–m^3 (3) 7·5–8·0 ; c–m^3 (5) 5·9–6·0 ; length of complete mandible (3) 11·2–11·6 ; c–m_3 6·5–6·6.

LITERATURE. Monard, 1935 : 52 (notes, description repeated, in French) ; Hill & Carter, 1941 : 52 (notes, descriptive data), 177 (measurements of Angolan specimen, from Monard).

DISTRIBUTION. KENYA (three examples collected in 1965 by A. N. Start in the Cherangani Hills, east of Mount Elgon, northeast of Kitale, Kenya, at 6000 feet, examined by R. W. Hayman : see Hayman & Hill, 1971 : 36, 37) ; ANGOLA (Monard, 1935 : 52 ; Hill & Carter, 1941 : 52, 177 ; Hayman, 1963 : 104) ; ZAMBIA (Wroughton, 1907 : 4 ; Lancaster, 1953 : 18, as *Scotoecus woodi*, identified as *Nycticeius hirundo hindei* (= *Scotoecus hindei hindei*) by Ansell, 1960 : 23, Appendix A, p. 110, Appendix B, p. 117 ; Ansell, 1967 : 21, as *S. hirundo hindei* (= *S. hindei hindei*). Hollister (1918 : 94) recorded *albigula* from Kiriba, Uganda, but Kock (1969 : 192) considers this to represent *S. hirundo hindei* (= *S. hindei hindei*) and notes that Kiriba is in the southern Sudan, 10 miles south of Gondokoro.

Remarks. The dimensions of B.M. 7.1.11.6 from Petauke, Zambia (Wroughton 1907 : 4), are similar to those of *S. h. albigula*, and this specimen has the generally heavier canines and more massive cheekteeth associated with this form, to which it is referred. Specimens in the Kaffrarian Museum (K.M. 1982, 1983) reported as *Scotoecus woodi* from the Fort Jameson District by Lancaster (1953 : 18) are identified as *S. hirundo hindei* (= *S. hindei hindei*) by Ansell (see above). These may in fact also be referable to *albigula*, and provisionally are listed as such here, as is a specimen reported from Mfuwe Camp, Zambia by Ansell, 1967 : 21 as *S. hirundo hindei* (= *S. hindei hindei*) but which is larger than this subspecies.

It is possible that further specimens may show *albigula* to be specifically distinct. It occurs as far north in Kenya as Mount Elgon and the Cherangani Hills, while *S. h hindei* has been obtained from more southerly localities in Katanga, Zaire and in Tanzania. However, in Kenya *albigula* has been reported only from high elevations, *S. h. hindei* only from lower altitudes, and direct sympatry has yet to be shown to occur.

Scotoecus hindei falabae Thomas, 1915

Scotoecus falabae Thomas, 1915 : 447. Kabwir, northern Nigeria, 2500 feet.

Diagnosis. Similar in most respects to *S. h. hindei* but slightly smaller and dorsally a little paler.

Measurements. Length of forearm (8) 32·0–35·2 ; greatest length of skull (7) 13·8–14·4 ; condylobasal length (6) 13·2–13·5 ; condylocanine length (6) 13·5–13·7 ; width of rostrum (7) 6·5–7·0 ; width across anteorbital foramina (7) 5·0–5·3 ; least interorbital width (7) 4·3–4·6 ; zygomatic width — ; width of braincase (6) 7·3–7·9 ; mastoid width (6) 8·4–9·0 ; c^1–c^1 (7) 4·7–5·0 ; m^3–m^3 (7) 6·6–6·9 ; c–m^3 (8) 5·2–5·5 ; length of complete mandible (5) 9·8–10·0 ; c–m_3 (7) 5·6–5·8.

Literature. Rosevear, 1965 : 300 (further description, as a species), 305, fig. 80b (tragus).

Distribution. Nigeria (Kabwir ; Yaba ; Jos, specimens in British Museum (Natural History)) ; Cameroon (Yagoua ; Mokolo (Mayo Louti), specimens obtained by F. de Vree and W. Verheyen).

Remarks. Specimens from the northern Cameroon are very similar in size to *S. h. falabae* from Nigeria but on the whole have slightly more massive canines and, to a lesser extent, more massive cheekteeth. In this respect they approach *S. h. hindei.*

There is apparently no sexual dimorphism in size either in *S. hirundo* or in *S. hindei* : however, female specimens in both have slightly smaller, more slender canines than do male examples. The canines of specimens attributed to *S. hirundo* are generally less massive than are those of specimens referred to *S. hindei*, but in the case of *S. hirundo* and *S. hindei falabae* the canines of males of *hirundo* are almost exactly similar in size to those of females of *falabae*.

The only localities at which specimens attributed to *S. hirundo* have been found so far to occur sympatrically with others referred to *S. hindei* are Yagoua, northern Cameroon (*Scotoecus* having been hitherto unreported from the Cameroon), and Didessa River, Wollega Province, Ethiopia, with near sympatry at other Ethiopian localities and in Uganda. From Yagoua, F. de Vree and W. Verheyen obtained four examples of *Scotoecus*, two males and two females. The two male specimens are quite clearly referable to *S. hindei falabae* with which they are in close agreement. The two female specimens have considerably shorter skulls and agree closely with females of *S. hirundo*. F. de Vree and W. Verheyen also obtained a male and female from Mokolo (Mayo Louti) but these are of similar size, agreeing in this respect with *falabae* to which they are referred. The females from Yagoua are smaller than the female of *falabae* from Mokolo and consequently are referred to *S. hirundo*. Measurements of these specimens, and of others from Ethiopia and Uganda, appear in Table 1.

TABLE

Measurements (in millimetres) of specimens from areas o

Registration No.	Sex	Length of forearm	Greatest length of skull	Condylo-basal length	Condylo-canine length	Rostral width	Width across anteorbital foramina	Least interorbit width
S. hirundo								
B.M. 72.4421	♀	31·7	12·6	12·4	12·3	6·1	4·6	4·2
B.M. 70.2267	♂	32·0	—	—	—	6·3	4·9	4·4
B.M. 70.2269	♂	31·1	13·1	12·7	12·6	6·5	5·2	4·2
B.M. 70.2263 70 2266 B.M. 70.2268 B.M. 70.2270	♀♀	29·7 –31·7 (6)	12·8 –13·4 (5)	12·1 –12·5 (5)	12·1 –12·5 (5)	6·1 –6·4 (6)	4·7 –5·0 (6)	4·2 –4·5 (6)
B.M. 72.4420*	♀	31·8	—	12·4	12·4	6·0	4·6	4·2
B.M. 74.4	♂	32·0	—	12·7	12·8	6·5	5·2	4·5
B.M. 74.1	♀	32·5	13·4	12·9	13·0	6·4	5·0	4·7
B.M. 74.2	♀	30·4						
B.M. 74.3	♀	30·8	13·2	12·5	12·6	6·2	4·6	4·4
B.M. 74.5*	♀	30·1						
1.430	♀	31·5	13·2	12·4	12·5	6·2	4·9	4·3
1.431	♀	32·8	13·5	12·7	12·9	6·0	4·8	4·3
S. hindei hindei								
B.M. 72.4423	♂	34·1	14·2	13·6	13·6	7·1	5·4	4·8
B.M. 70.2262	♂	37·2	14·8	14·2	14·2	6·7	5·3	4·6
B.M. 72.4422	♂	33·4	—	13·6	13·5	—	—	4·6
B.M. 63.1151	♂	—	14·4	13·9	13·8	6·6	5·3	4·6
B.M. 65.3435	♂	32·7	14·2	13·7	13·9	6·7	5·3	4·7
S. hindei falabae								
1.415	♂	32·9	13·8	13·4	13·5	6·5	5·0	4·4
1.429	♂	32·6	13·9	13·3	13·5	6·8	5·2	4·3
1.667	♂	32·0	14·0	13·2	13·5	7·0	5·2	4·5
1.682	♀	33·5	13·9	13·2	13·6	6·5	5·1	4·4

* Young adult

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mpatry or near sympatry between *S. hirundo* and *S. hindei*

gomatic width	Width of braincase	Mastoid width	c^1–c^1	m^3–m^3	c–m^3	Length of complete mandible	c–m_3	Location
—	7·1	8·2	4·3	6·0	4·7	—	4·9	Didessa, Ethiopia
—	7·5	—	4·7	6·6	4·9	—	5·3	Gambela, Ethiopia
—	7·2	8·3	4·8	6·6	5·0	9·4	5·3	Gambela, Ethiopia
—	7·3 –7·5 (4)	8·2 –8·3 (5)	4·6 –4·7 (6)	6·3 –6·5 (6)	4·7 –4·8 (6)	8·9 –9·9 (6)	4·9 –5·2 (6)	Gambela, Ethiopia
—	7·0	7·7	4·3	5·9	4·7	9·1	5·1	Gambela, Ethiopia
—	7·5	—	4·8	6·3	5·1	9·9	5·5	Budongo, Uganda
—	7·6	—	4·7	6·6	5·1	9·6	5·3	Budongo, Uganda
								Budongo, Uganda
—	7·1	8·3	4·6	6·3	4·8	9·4	5·1	Budongo, Uganda
								Budongo, Uganda
—	7·3	8·3	4·5	6·6	4·9	9·0	5·2	Yagoua, Cameroon
—	7·3	8·2	4·5	6·7	5·0	9·6	5·4	Yagoua, Cameroon
—	7·5	8·9	5·1	6·9	5·3	10·0	5·6	Didessa, Ethiopia
—	7·8	9·4	5·2	7·0	5·7	10·6	6·1	Bulcha, Ethiopia
—	7·9	8·8	—	—	5·4	—	5·8	Bulcha, Ethiopia
—	7·3	8·8	5·3	6·9	5·3	10·3	5·7	West Madi, Uganda
—	8·0	9·2	5·2	6·5	5·4	10·6	5·8	Nabumali, Uganda
—	7·5	8·4	4·8	6·7	5·5	10·0	5·8	Yagoua, Cameroon
10·1	7·3	8·6	5·0	6·9	5·3	10·0	5·8	Yagoua, Cameroon
—	7·4	8·6	4·9	6·7	5·2	9·8	5·6	Mokolo (Mayo Louti), Cameroon
10·0	7·4	8·9	4·7	6·8	5·3	10·0	5·7	Mokolo (Mayo Louti), Cameroon

SUMMARY

The vespertilionid genus *Scotoecus* is reviewed in detail, and is considered to include four species, one, *pallidus*, from India, having been referred at one time to *Scoteinus* and more recently to *Nycticeius*. The three remaining, *albofuscus*, *hirundo* and *hindei* are African: evidence is brought forward to support the view that *hirundo* and *hindei* are specifically distinct, not conspecific as thought by the majority of modern authors. Both are reported for the first time from the Cameroon and from Ethiopia.

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BULLETIN OF
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CATALOGUE OF THE TYPES OF TERRESTRIAL ISOPODS (ONISCOIDEA) IN THE COLLECTIONS OF THE BRITISH MUSEUM (NATURAL HISTORY)

I. SUPERFAMILY PSEUDOTRACHEATA

By ROGER J. LINCOLN AND JOAN P. ELLIS

THE superfamily Pseudotracheata comprises the following ten families of terrestrial isopods: Cylisticidae, Porcellionidae, Balloniscidae, Trachelipidae, Atlantidiidae, Armadillidiidae, Eubelidae, Sphaeroniscidae, Actoeciidae, Armadillidae, encompassing all those groups of woodlice which possess the characteristic pseudotracheal respiratory apparatus (Vandel, 1962, 1963, 1968, 1970).

The collections of the British Museum (Natural History) are very rich in type material of this group of woodlice, acquired in large part from the extensive collections of Gustave Budde-Lund, A. M. Norman and Karl W. Verhoef, and to a lesser extent from C. L. Koch, Adrien Dollfus, J. Omer-Cooper, K. H. Barnard, W. E. Collinge and others. This important collection of types has now been indexed and catalogued for the first time, and it is hoped at a future date to provide a similar catalogue listing the rest of the holdings of woodlice types.

The catalogue contains in all some 672 separate items relating to 522 species in 77 genera. The genera are listed alphabetically within families, and the species are similarly listed within the appropriate genus. All available information, including the reference to the original description, number and sex of specimens, type status, locality, date, collector, method of acquisition and British Museum (Natural History) registration number, is given with each item. Unless otherwise stated the material is preserved in spirit.

Where the author's name appears in brackets it indicates that the entry is made in a combination other than the original combination, in which case the latter is given in square brackets thus:

albicornis (Dollfus) (1896b : 3) [*Lucasius albicornis*]

Where a particular species is now considered a junior synonym of another species the latter is also indicated in brackets after the entry:

sphinx Verhoeff (1931a : 533) [Transferred to *Porcellio lamellatus* Uljanin]

A full index of species, genera and families is provided at the end of the catalogue.

The collection also contains a large number of specimens labelled as types, mostly from the Budde-Lund collection, for which no reference can be found in published literature. It seems probable that these are specimens with manuscript names which have been incorporated into personal collections but which have never been published. A list of this material comprising 167 items is given in Appendix 1, and a list of the manuscript names has been deposited in the library of the British Museum (Natural History).

Family **CYLISTICIDAE**

CYLISTICUS Schnitzler

annulicornis Verhoeff (1908b : 184)

SYNTYPES : three females. Reg. no. 1907:11:4:36–38. Toscana region, Italy. Purchased from K. W. Verhoeff.

biellensis Verhoeff (1930a : 176)

SYNTYPES : two females. Reg. no. 1930:5:26:54–55. Piemonte, Italy. Purchased from K. W. Verhoeff.

SYNTYPES : two males ; six females. Reg. no. 1937:7:6:109–113. Piemonte, Italy. Purchased from K. W. Verhoeff.

caucasius Verhoeff (1917 : 157)

SYNTYPES : male. Reg. no. 1921:6:10:46. Gagri, Caucasus Mts. Collected by N. Lignau. Purchased from K. W. Verhoeff.

dentifrons Budde-Lund (1885 : 81)

HOLOTYPE : fragments. Reg. no. 1921:10:18:4212. Astrakhan, USSR. Budde-Lund Collection.

esterelanus Verhoeff (1917 : 155)

SYNTYPE : female. Reg. no. 1921:6:10:45. Estérel Mts, France. Purchased from K. W. Verhoeff.

gracilipennis Budde-Lund (1885 : 79, 229)

SYNTYPE : male. Reg. no. 1911:11:8:10063. Rome, Italy. Collected by Bergsøe. Norman Collection (ex Copenhagen Museum).

SYNTYPE : male. Reg. no. 1921:10:18:4213. (Redetermined as *Cylisticus esterelanus* Verhoeff.) Pierrefeu, France. Collected by E. Simon. Budde-Lund Collection.

SYNTYPES : three males ; three females. Reg. no. 1921:10:18:2414–4218. Rome, Italy. Collected by Bergsøe. Budde-Lund Collection.

SYNTYPES : one male ; one female. Reg. no. 1956:10:10:201–202. Rome, Italy. Collected by Bergsøe. Presented by University College, Dundee.

nasatus Verhoeff 1931a : 527

SYNTYPE : one juvenile. Reg. no. 1931:4:27:42. Villa Napoleon, Elba I. Collected by K. Strasser. Purchased from K. W. Verhoeff.

SYNTYPE : female. Reg. no. 1930:5:26:52. Ormea, Liguria, Italy. Purchased from K. W. Verhoeff.

pallidus Verhoeff (1928c : 159)

SYNTYPE : female. Reg. no. 1930:5:26:53. Liguria, Italy. Purchased from K. W. Verhoeff.

plumbeus Verhoeff (1901b : 73)

SYNTYPE : female. Reg. no. 1901:9:19:41. Lake Garda, Italy, Purchased from K. W. Verhoeff.

plumbeus bergomatius Verhoeff (1928c : 162)

SYNTYPES : one male ; one female. Reg. no. 1928:7:4:107–108. Bergamo, Italy. Purchased from K. W. Verhoeff.

plumbeus umbricus Verhoeff (1928c : 163)

SYNTYPES : one male ; one female. Reg. no. 1928:7:4:105–106. Umbria, Italy. Purchased from K. W. Verhoeff.

pontremolensis Verhoeff (1936a : 112)

SYNTYPES : one male ; three females. Reg. no. 1937:7:6:114–117. Spezia, N. Italy. Purchased from K. W. Verhoeff.

suberorum Verhoeff (1931a : 526)

SYNTYPE : juvenile. Reg. no. 1931:4:27:41. Monte Massoncello, Italy. Purchased from K. W. Verhoeff.

transsilvaticus Verhoeff (1908b : 185)

SYNTYPE : female. Reg. no. 1907:11:4:39. Siebenbürgens. Purchased from K. W. Verhoeff.

Family **PORCELLIONIDAE**

ACAEROPLASTES Verhoeff

argentarius (Verhoeff) (1931a : 541) [*Metoponorthus* (*A.*) *argentarius*]

SYNTYPE : female. Reg. no. 1931:4:27:62. Monte Argentario, Italy. Purchased from K. W. Verhoeff.

melanurus (Budde-Lund) (1885 : 181) [*Metoponorthus melanurus*]

SYNTYPES : two females. Reg. no. 1921:10:18:5273–5274. Porto Calvien, Corsica. Collected by E. Simon. Budde-Lund Collection.

SYNTYPES : two males; one female. Reg. no. 1956:10:10:145–146. Bona, Algeria. Collected by Meinert. Presented by University College, Dundee.

AGABIFORMIUS Verhoeff

hirtus (Aubert & Dollfus) (1890 : 8) [*Lucasius hirtus*]

SYNTYPE : male. Reg. no. 1911:11:8:10532. Marseille, France. 'In soil at the foot of a wall.' Collected by A. Dollfus. Norman Collection.

SYNTYPE : female. Reg. no. 1921:10:18:4023. Marseille, France. Budde-Lund Collection.

minutus (Budde-Lund) (1909a : 8) [*Angara minuta*]

SYNTYPES : three females. Reg. no. 1921:10:18:4028–4030. Porto Tunis, Tunisia. Collected by F. Silvestri. Budde-Lund Collection.

SYNTYPES : one male; one female. Reg. no. 1921:10:18:4031–4032. Sidi Bel Akaren. Collected by F. Silvestri. Budde-Lund Collection.

obtusus (Budde-Lund) (1909a : 8) [*Angara obtusa*]

SYNTYPES : one male; four females. Reg. no. 1921:10:18:4061–4065. Cairo, UAR. 18.5.1901. Collected by L. A. Jägerskjöld. Budde-Lund Collection.

rufobrunneus Omer-Cooper (1923 : 401)

SYNTYPE : fragments. Reg. no. 1922:5:18:6. Amara, Iraq. 13.2.1918. Collected by W. E. Evans. Presented by J. Omer-Cooper.

SYNTYPES : micropreparations of appendages : six males, one female. Reg. no. 1922:5:18:51–57. Amara, Iraq. 13.2.1918. Collected by W. E. Evans. Presented by J. Omer-Cooper.

CAEROPLASTES Verhoeff

porphyrivagus (Verhoeff) (1918 : 134) [*Metoponorthus* (*C.*) *porphyrivagus*]

SYNTYPE : female. Reg. no. 1921:6:10:31. French Riviera. Purchased from K. W. Verhoeff.

DESERTONISCUS Verhoeff

subterraneus Verhoeff (1930b : 120)

SYNTYPE : female. Reg. no. 1930:5:26:73. Turkestan, USSR. Purchased from K. W. Verhoeff.

ENNURENSIS Collinge

hispidus Collinge (1915a : 143)

PARATYPE : female. Reg. no. 1919:4:26:519. Ennur, near Madras, India. 'Under stones on sand 19.10.1913.' Collected by N. Annandale. Collinge Collection.

GERUFA Budde-Lund

hirticornis Budde-Lund (1909b : 59)

SYNTYPES : two females. Reg. no. 1921:10:18:1468–1469. Cape Flats, South Africa. Collected by L. Schultze. Budde-Lund Collection.

macrops Barnard (1932 : 276)

SYNTYPES : four males ; nineteen females. Reg. no. 1933:1:25:208–215. Oudebosch, River Zonder End Mts, Cape Province, South Africa. Collected by K. H. Barnard. Presented by the South African Museum.

marmorata Barnard (1932 : 277)

SYNTYPES : four males ; thirty-six females. Reg. no. 1933:1:25:216–227. George, Cape Province, South Africa. Collected by K. H. Barnard. Presented by the South African Museum.

montana Barnard (1932 : 275)

SYNTYPES : five females. Reg. no. 1933:1:25:204–207. Riversdale Mts, Cape Province, South Africa. Collected by K. H. Barnard. Presented by the South African Museum.

HALOPORCELLIO Verhoeff

penicilliger Verhoeff (1917 : 170)

HOLOTYPE : male. Reg. no. 1921:6:10:78. Yafo, Israel. Collected by Aharoni. Purchased from K. W. Verhoeff.

sphinx Verhoeff (1931a : 533) [Transferred to *Porcellio lamellatus* Uljanin]

SYNTYPE : female. Reg. no. 1931:4:27:61. Populonia, Massoncella, Italy. Purchased from K. W. Verhoeff.

HEMILEPISTUS Budde-Lund

bodenheimeri Verhoeff (1931b : 40) [Transferred to *Hemilepistus reaumuri* (Audouin & Savigny)]

SYNTYPE : female. Reg. no. 1931:4:27:68. Palestine. Collected by Bodenheimer. Purchased from K. W. Verhoeff.

SYNTYPES : one male ; three females. Reg. no. 1938:7:7:41–44. Palestine. Collected by Bodenheimer. Purchased from K. W. Verhoeff.

cristatus Budde-Lund (1885 : 153)

SYNTYPES : one male ; three females. Reg. no. 1911:11:8:10443–10446. Serdscen, Iran. Norman Collection.

SYNTYPES : one male ; one female. Reg. no. 1956:10:10:156–157. Serdscen, Iran. Presented by University College, Dundee.

elongatus Budde-Lund (1885 : 160)

HOLOTYPE : female. Reg. no. 1921:10:18:4103. 'Taschburun in Transcaucasius.' June 1879. Collected by A. Brandt. Budde-Lund Collection.

nodosus Budde-Lund (1885 : 159)

SYNTYPES : one male ; one female. Reg. no. 1921:10:18:4115–4116. 'Tschinas, Rossia Asiatica.' 1878. Collected by V. Russow. Budde-Lund Collection.

palaestinus Verhoeff (1931b : 38)

SYNTYPES : two males. Reg. no. 1931:4:27:65–67. Palestine. Purchased from K. W. Verhoeff.

SYNTYPES : three males ; three females. Reg. no. 1938:7:7:35–40. Palestine. Purchased from K. W. Verhoeff.

schirasi Lincoln (1970 : 127)

PARATYPE : male. Reg. no. 1970:199:1. Shiraz, Iran. Collected by Kollar. Budde-Lund Collection.

zachvatkini Verhoeff (1930b : 122) [Transferred to *H. nodosus* Budde-Lund]

SYNTYPE : female. Reg. no. 1930:5:26:74. Turkestan, USSR. Purchased from K. W. Verhoeff.

HEMIPORCELLIO Collinge

carinatus Collinge (1915a : 145)

PARATYPE : female. Reg. no. 1919:4:26:458. Lake Chilka, Rambha, Ganjam District, Madras, India. 'At edge of Lake, 1913.' Collinge Collection.

immsi (Collinge) (1914a : 207) [*Porcellio immsi*]

HOLOTYPE : female. Reg. no. 1914:8:26:1. Allahabad, India. 16.9.1907. Collected and presented by A. D. Imms.

PARATYPES : one male ; one juvenile female. Reg. no. 1919:4:26:456–457. Allahabad, India. 16.9.1907. Collected by A. D. Imms. Collinge Collection.

INCHANGA Barnard

natalensis Barnard (1932 : 278)

SYNTYPES : five males ; eleven females. Reg. no. 1933:1:25:228–233. Inchanga, Natal, South Africa. 1917. Collected by K. H. Barnard. Presented by the South African Museum.

LEPTOTRICHUS Budde-Lund

politus Omer-Cooper (1923 : 402)

SYNTYPES : three males ; one female. Reg. no. 1922:5:18:7–10. Amara, Iraq. 1918. Collected by R. G. Tame. Presented by J. Omer-Cooper.

SYNTYPES : micropreparations of appendages : three males ; six females. Reg. no. 1922:5:18:35–43. Amara, Iraq. 1918. Collected by R. G. Tame. Presented by J. Omer-Cooper.

LUCASIUS Kinahan

pallidus (Budde-Lund) (1885 : 134) [*Porcellio pallidus*]

SYNTYPE : male. Reg. no. 1921:10:18:5182. Algier. Budde-Lund Collection.

SYNTYPES : three males. Reg. no. 1921:10:18:5183–5185. Tlemcen, Algeria. Collected by E. Simon. Budde-Lund Collection.

SYNTYPE : female. Reg. no. 1921:10:18:5186. Mid-France. Collected by E. Simon. Budde-Lund Collection.

MAHEHIA Budde-Lund

bicornis Budde-Lund (1913 : 376)

SYNTYPES : one male ; two females. Reg. no. 1913:1:8:64–66. Silhouette I., Seychelles, Indian Ocean. Collected by the 'Sealark' Expedition. Presented by J. S. Gardiner.

SYNTYPES : Seven males ; seven females. Reg. no. 1921:10:18:997–1008. Silhouette I., Seychelles, Indian Ocean. Budde-Lund Collection.

laticauda Budde-Lund (1913 : 376)

SYNTYPES : six males ; one female. Reg. no. 1913:1:8:58–63. Cascade, Mt Alphonse, Mahé I., Seychelles, Indian Ocean. 1800 ft, 'in base of *Pandanus* leaf'. Collected by the 'Sealark' Expedition. Presented by J. S. Gardiner.

maculata Budde-Lund (1913 : 375)

SYNTYPE : female. Reg. no. 1913:1:8:50. Mt Alphonse, Mahé I., Seychelles, Indian Ocean. 3.12.1905. Collected by the 'Sealark' Expedition. Presented by J. S. Gardiner.

SYNTYPE : female. Reg. no. 1921:10:18:1021. Top of Mt Morne, Mahé I., Seychelles, Indian Ocean. 2700 ft. Budde-Lund Collection.

SYNTYPE : few fragments only. Reg. no. 1921:10:18:1022. Seychelles, Indian Ocean. Budde-Lund Collection.

METOPONORTHUS Budde-Lund

approximatus Budde-Lund (1885 : 185)

SYNTYPE : male. Reg. no. 1921:10:18:5230. Sebastopol. Budde-Lund Collection.

benaci L. Koch (1901 : 56)

SYNTYPES : one male ; three females. Reg. no. 1925:7:22:697–700. Torbole, Italy. Koch Collection.

cilicius Verhoeff (1918 : 138)

SYNTYPE : female. Reg. no. 1921:6:10:35. Toros Gari Mts, Cilicia, Turkey. Purchased from K. W. Verhoeff.

coxalis Budde-Lund (1885 : 175)

SYNTYPE : female. Reg. no. 1911:11:8:10520. 'Ouled Anteurs', Algeria. Collected by E. Simon. Norman Collection.

SYNTYPES : one male ; two females. Reg. no. 1921:10:18:5235–5237. 'Rochers des Ouled Anteurs', Algeria. Collected by E. Simon. Budde-Lund Collection.

frontosus Budde-Lund (1885 : 183)

SYNTYPE : male. Reg. no. 1911:11:8:10525. Biskra, Algeria. Collected by Meinert. Norman Collection (ex E. Simon collection).

SYNTYPES : one male ; one female. Reg. no. 1921:10:18:5239–5240. Collected by Meinert. Budde-Lund Collection.

fuscomarmoratus Budde-Lund (1885 : 189)

SYNTYPE : female. Reg. no. 1911:11:8:10521. Oran, Algeria. Collected by E. Simon. Norman Collection.

SYNTYPES : three females. Reg. no. 1921:10:18:5241–5243. Oran, Algeria. Collected by E. Simon. Budde-Lund Collection.

gravei Verhoeff (1918 : 135)

SYNTYPE : male. Reg. no. 1921:6:10:36. Sicily. Purchased from K. W. Verhoeff.

hispida (Miers) (1877b : 676) [*Porcellio* (*Porcellionides*) *hispida*]

SYNTYPES : one male ; one female. Reg. no. 1879 : 21. Mongolia. Presented by Prof. Wrzésniowsky.

lacteolus Budde-Lund (1885 : 186)

SYNTYPE : female. Reg. no. 1911:11:8:10492. 'Bou-Saada', Algeria. Collected by E. Simon. Norman Collection.

SYNTYPES : one male ; one female. Reg. no. 1921:10:18:4400. 'Bou-Saada', Algeria. Collected by E. Simon. Budde-Lund Collection.

littoralis Budde-Lund (1885 : 179)

SYNTYPES : one male ; one female. Reg. no. 1921:10:18:5247–5248. 'Kertsch', Crimea. Collected by V. N. Uljanin. Budde-Lund Collection.

SYNTYPES : two males ; one female. Reg. no. 1921:10:18:5249–5251. (Redetermined *Protracheoniscus occidentalis* Vandel.) Montpellier, France. Collected by E. Simon. Budde-Lund Collection.

SYNTYPES : one male ; one female. Reg. no. 1921:10:18:5252–5253. Crimea, Ukraine, USSR. Collected by V. N. Uljanin. Budde-Lund Collection.

myrmicidarum Verhoeff (1918 : 132) [Transferred to *M.* (*Myrmeconiscus*) *myrmecophilus myrmecophilus* (Stein)]

SYNTYPES : one male ; one female. Reg. no. 1921:6:10:37–38. Sicily. Purchased from K. W. Verhoeff.

nigrobrunneus Budde-Lund (1896 : 47)

SYNTYPE : head only (both antennae and mouthparts from right-hand side missing). Reg. no. 1921:10:18:5328. Kappari, Greece. 14.6.1887. Collected by Oertzen. Budde-Lund Collection.

philoscoides Budde-Lund (1885 : 175)

SYNTYPES : three females. Reg. no. 1911:11:8:10506–10508. Algeria. Collected by E. Simon. A. M. Norman Collection (ex Dollfus collection).

SYNTYPES: six females. Reg. no. 1921:10:18:5329–5334. Oned-Zitoun, Algeria. May 1883. Collected by E. Simon. Budde-Lund Collection.

SYNTYPES: two males; one female. Reg. no. 1928:12:1:1518–1520. Algeria. Collected by E. Simon. Stebbing Collection (ex Dollfus collection).

SYNTYPES: two females. Reg. no. 1956:10:10:141–142. Oned-Zitoun, Algeria. Collected by E. Simon. Presented by University College, Dundee.

pruinosus anconanus Verhoeff (1928c : 144)

SYNTYPE: male. Reg. no. 1928:7:4:89. Ancona, Italy. Purchased from K. W. Verhoeff.

SYNTYPES: two males; one female. Reg. no. 1973:152:3. Mid-Italy. Larwood Collection (ex Verhoeff collection).

pruinosus meleagris Budde-Lund (1885 : 168) [*Metoponorthus meleagris*]

SYNTYPES: two males; seven females. Reg. no. 1921:10:18:5279–5287. France ('Gallia Meridionalis'). Collected by E. Simon. Budde-Lund Collection.

sabuleti Budde-Lund (1885 : 186)

SYNTYPES: one male; one female. Reg. no. 1921:10:18:3920–3921. Biskra, Algeria. Budde-Lund Collection.

SYNTYPES: two females. Reg. no. 1921:10:18:3922–3923. Algeria. Budde-Lund Collection.

SYNTYPE: male. Reg. no. 1921:10:18:4735. Biskra Mt, Algeria. Collected by Tatschanowski. Budde-Lund Collection.

sexfasciatus Budde-Lund (1885 : 167)

SYNTYPES: five females. Reg. no. 1921:10:18:5306–5310. Algiers. Collected by E. Simon. Budde-Lund Collection.

sexfasciatus asifensis Verhoeff (1938b : 63) [*Metoponorthus asifensis*]

SYNTYPE: female. Reg. no. 1938:7:7:45. Atlas, Morocco. Purchased from K. W. Verhoeff.

virgatus Budde-Lund (1885 : 182)

SYNTYPES: two males; nine females. Reg. no. 1921:10:18:5514–5525. Florida, N. America. Collected by Leuckart. Budde-Lund Collection.

viridis Budde-Lund (1885 : 179)

SYNTYPES: three males. Reg. no. 1921:10:18:5526–5527. Bona, Algeria. Collected by E. Meinert. Budde-Lund Collection.

MICA Budde-Lund

tardus (Budde-Lund) (1885 : 305) [*Porcellio tardus*]

SYNTYPE: female. Reg. no. 1911:11:8:10533. Tlemcen, Algeria. Collected by E. Simon. Norman Collection.

PORCELLIO Latreille

acustiserra Barnard (1940 : 358)

SYNTYPES: thirteen males; twenty females. Reg. no. 1949:2:2:138–162. Lakes of Addas, shore of Hora Harsadi, Ethiopia, 7000 ft. 3.12.1936. Collected and presented by J. Omer-Cooper.

aegaeus Verhoeff (1907a : 257)

SYNTYPE: female. Reg. no. 1907:11:4:44. Naxós I., Greece. Purchased from K. W. Verhoeff.

albicornis (Dollfus) (1896b : 3) [*Lucasius albicornis*]

SYNTYPE: male. Reg. no. 1911:11:8:10529. Ficuzza, Palermo, Sicily. 900 m. Norman Collection (ex Dollfus collection).

SYNTYPES: not separated from other (non-type) specimens. Reg. no. 1921:10:18:5163–5172 (part). Ficuzza, Palermo, Italy. Budde-Lund Collection (ex Dollfus collection).

albinus Budde-Lund (1885 : 142)

SYNTYPE : male. Reg. no. 1921:10:18:5163. Onargla, Sahara, Algeria. Collected by E. Simon. Budde-Lund Collection.

albomarginatus Vogl (1875 : 516)

SYNTYPES : four males. Reg. no. 1925:7:22:449–451. Syra I., Cyclades, Greece. Collected by Ebner. Koch Collection.

alluaudi Dollfus (1893 : 52)

SYNTYPES : two males. Reg. no. 1921:10:18:4249–4250. Canary Is. Collected by C. Alluaud. Budde-Lund Collection.

amoenus Dollfus (1829b : 178) [Transferred to *Porcellio violaceus* Budde-Lund]

SYNTYPES : two males ; one female. Reg. no. 1911:11:8:10396–10398. Cuenca, Spain. Norman Collection.

angustulus Budde-Lund (1885 : 146)

SYNTYPE : female. Reg. no. 1911:11:8:10429. Bou-Saada, Algeria. Collected by E Simon. Norman Collection (ex Dollfus collection).

SYNTYPES : one male ; four females. Reg. no. 1921:10:18:3792–3796. Algeria. Collected by E. Simon. Budde-Lund Collection.

ater Budde-Lund (1896 : 45)

SYNTYPES : one male ; one female. Reg. no. 1921:10:18:4284–4285. Rothenthurm Pass, Transylvania, Rumania. Budde-Lund Collection.

auritus Budde-Lund (1885 : 126)

SYNTYPE : female. Reg. no. 1921:10:18:4978. Seville, Spain. Collected by Fr. Meinert. Budde-Lund Collection.

barroisi Dollfus (1892c : 127)

SYNTYPE : female. Reg. no. 1911:11:8:10400. 'Ouadys de la Mer Morte.' Collected by T. Barrois. Norman Collection (ex Dollfus collection)

batesoni Collinge (1915b : 461)

PARATYPE : male. Reg. no. 1919:4:26:540. S. Spain, 1894. Collected by W. Bateson. Collinge Collection.

bistriatus Budde-Lund (1885 : 88)

SYNTYPE : male. Reg. no. 1921:10:18:4288. Istanbul, Turkey. Collected by Jelski. Budde-Lund Collection.

blattarius Budde-Lund (1885 : 131)

SYNTYPE : male. Reg. no. 1921:10:18:4286. Algeria. Budde-Lund Collection.

brevipennis Budde-Lund (1885 : 97)

SYNTYPES : one male ; three females. Reg. no. 1921:10:18:3798–3801. Algeria. Collected by E. Simon. Budde-Lund Collection.

buddelundi Simon (1885 : 10)

SYNTYPE : female. Reg. no. 1911:11:8:10428. Tunisia. Norman Collection (ex Dollfus collection).

SYNTYPES : two males ; one female. Reg. no. 1921:10:19:4979–4981. Tunisia. Budde-Lund Collection (ex Simon collection).

calmani Omer-Cooper (1923 : 399)

SYNTYPES : two females. Reg. no. 1922:5:18:4–5. Baku, Azerbaydzhan, USSR. Collected by P. A. Buxton. Presented by J. Omer-Cooper.

canariensis Dollfus (1893 : 50)

SYNTYPE : male. Reg. no. 1911:11:8:10409. Canary Is. Collected by C. Alluaud. Normal Collection (ex Dollfus collection).

SYNTYPES : two males ; one female ; one juvenile. Reg. no. 1921:10:18:4289–4291. Canary Is. Collected by C. Alluaud. Budde-Lund Collection.

carthaginensis Silvestri (1897 : 415) [Transferred to *Porcellio olivieri* Audouin]

SYNTYPES : four males ; seven females. Reg. no. 1921:10:18:3802–3811. Carthage (ruins), Tunisia. Budde-Lund Collection.

cayennensis Miers (1877b : 667) [Transferred to *Porcellio scaber* Latreille]

SYNTYPES : two females. Reg. no. 1941:6:27:15. Cayenne, Guiana. Presented by Prof. Wrzésniowsky.

cognatus L. Koch (1901 : 52)

SYNTYPE : female. Reg. no. 1925:7:22:453–454 (part). Meran Molde. Koch Collection.

SYNTYPE : female. Reg. no. 1925:7:22:453–454 (part). Ratzes. Koch Collection.

contractus Dollfus (1892c : 8)

SYNTYPE : male. Reg. no. 1892:12:6:1. Syria. Presented by W. D'Arcy Thompson.

SYNTYPES : one male ; one female. Reg. no. 1911:11:8:10384–10385. Syria. Collected by L. Bleuse. Norman Collection.

SYNTYPES : two males. Reg. no. 1928:12:1:1464–1465. Saida, Syria. Collected by L. Bleuse. Stebbing Collection.

cruentatus L. Koch (1901 : 37)

SYNTYPES : one male ; one female. Reg. no. 1925:7:22:479–480. Sugenheim, W. Germany. Koch Collection.

debueni Dollfus (1892b : 176)

SYNTYPES : three females. Reg. no. 1911:11:8:10393–10395. Villa Rutis, Coruna, Spain. Collected by Bolivar. Norman Collection.

SYNTYPE : female. Reg. no. 1921:10:18:4360. Coruna, Spain. Collected by Bolivar. Budde-Lund Collection.

dispar Verhoeff (1901d : 407)

SYNTYPES : one male ; two females. Reg. no. 1901:9:19:86–88. Coimbra, Portugal. Collected by Moller. Purchased from K. W. Verhoeff.

SYNTYPE : female. Reg. no. 1907:11:4:72. Coimbra, Portugal. Collected by Moller. Purchased from K. W. Verhoeff.

evansi Omer-Cooper (1923 : 398)

HOLOTYPE : male. Paratypes : one male ; one female. Reg. no. 1922: 5:18:1–3. Amara, Mesopotamia, Iraq. Collected by C. L. Boulenger. Presented by J. Omer-Cooper.

PARATYPES : micropreparations of appendages : two males ; five females. Reg. no. 1922:5:18:44–50. Amara, Iraq. Collected by C. L. Boulenger. Presented by J. Omer-Cooper.

ficorum Verhoeff (1931a : 532)

SYNTYPE : male. Reg. no. 1931:4:27:57. Monte Massoncello, Italy. Purchased from K. W. Verhoeff.

ficulneus Budde-Lund (1885 : 98)

SYNTYPES : two males ; two females. Reg. no. 1921:10:18:4995–4998. Syria. Collected by E. Simon. Budde-Lund Collection.

SYNTYPES : two females. Reg. no. 1956:10:10:228–229. Syria. Collected by E. Simon. Presented by University College, Dundee.

flavocinctus Budde-Lund (1885 : 109)

SYNTYPES : two females. Reg. no. 1956:10:10:226–227. Spain. Collected by L. Lund and Fr. Meinert. Presented by University College, Dundee.

flavovittata Miers (1877b : 669) [Transferred to *Metoponorthus pruinosus* (Brandt)]

SYNTYPES : four females. Reg. no. 1879:21. Cayenne, Guiana. Presented by Prof. Wrzésniowsky.

gallicus Dollfus (1903 : 63)

SYNTYPES : two females. Reg. no. 1907:11:4:73–74. Pyrénées. Purchased from K. W. Verhoeff.

gemmulatus Dana (1853 : 725) [Transferred to *Porcellio scaber* Latreille]

SYNTYPES : five males ; one female. Reg. no. 1877:3. San Francisco, N. America. Presented by W. N. Lockington.

graniger Miers (1876 : 226)

HOLOTYPE : female. Reg. no. 1973:512:1 (original registration no. 1854:4). New Zealand. Presented by Col. Bolton.

granuliferus Budde-Lund (1885 : 128)

Syntypes : one female ; one juvenile. Reg. no. 1921:10:18:3812. Spain. Collected by L. Lund. Budde-Lund Collection.

imbutus Budde-Lund (1885 : 145)

Syntypes : not separated from other (non-type) specimens. Reg. no. 1921:10:18:4425–4436 (part). Sicily. Budde-Lund Collection.

imbutus pellegrinensis Verhoeff (1908a : 366)

Syntype : male. Reg. no. 1921:6:10:32. Sicily. Purchased from K. W. Verhoeff.

incanus Budde-Lund (1885 : 102)

Syntypes : two females. Reg. no. 1921:10:18:4437–4438. Spain. Collected by Fr. Meinert. Budde-Lund Collection.

intercalarius Budde-Lund (1885 : 104)

Syntype : female. Reg. no. 1921:10:18:4439. Bona, Algeria. Collected by Fr. Meinert. Budde-Lund Collection.

interpolator Budde-Lund (1885 : 93)

Syntypes : specimens coated with mould. Reg. no. 1921:10:18:4632–4633. 'Ordus.' Budde-Lund Collection.

jelskii Miers (1877b : 668) [Transferred to *Metoponorthus pruinosus* Brandt]

Syntypes : one male ; two females. Reg. no. 1879:21. Maraynioe (?), Guiana. Presented by Prof. Wrzésniowsky.

Syntypes : three males ; three females. Reg. no. 1879:21. Pumamarca, Peru. Presented by Prof. Wrzésniowsky.

Syntypes : nine males ; ten females. Reg. no. 1887:20. Caracas, Guiana. Presented by Dr Ernst.

latissimus Budde-Lund (1885 : 95) [Transferred to *Porcellio spatulatus* (Costa)]

Syntypes : three males ; five females. Reg. no. 1921:10:18:4988–4992. Corsica (collected by E. Simon) and Sardinia (collected by Keitel). Budde-Lund Collection.

lepineyi Verhoeff (1937b : 305)

Syntypes : one male ; three females. Reg. no. 1938:7:7:7–10. Haute Atlas, Morocco. Collected by J. de Lépiney. Purchased from K. W. Verhoeff.

longicauda Budde-Lund (1885 : 112)

Syntype : male. Reg. no. 1911:11:8:10358. Algeria. Collected by Fr. Meinert. Norman Collection.

Syntypes : two females. Reg. no. 1911:11:8:10359–10360. Algeria. Collected by E. Simon. Norman Collection.

Syntypes : one male ; five females. Reg. no. 1921:10:18:4466–4471. Algeria. Budde-Lund Collection.

Syntypes : one male ; one female. Reg. no. 1956:10:10:230–231. Algeria. Presented by University College, Dundee.

longipennis Budde-Lund (1885 : 91)

Syntypes : two females. Reg. no. 1921:10:18:4475–4476. Avhasia, Caucasus Mts. Collected by Nordmann. Budde-Lund Collection.

maculipes Budde-Lund (1885 : 105)

Syntypes : two males ; two females. Reg. no. 1921:10:18:4488–4491. Madeira I. Collected by Sørensen. Budde-Lund Collection.

magnificus Dollfus (1892b : 170)

Syntype : female. Reg. no. 1911:11:8:10430. Alcazaba, Almeria, Spain. Collected by R. Nickles. Norman Collection (ex Dollfus collection).

Syntype : female. Reg. no. 1921:10:18:4492. Alcazaba, Almeria, Spain. Collected by R. Nickles. Budde-Lund Collection (ex Dollfus collection).

marginenotatus Budde-Lund (1885 : 145)

Syntype : male. Reg. no. 1921:10:18:4500. Bona, Algeria. Collected by Fr. Meinert. Budde-Lund Collection.

SYNTYPE: female. Reg. no. 1956:10:10:223. Bona or Constantine, Algeria. Collected by Fr. Meinert. Presented by University College, Dundee.

mildei L. Koch (1901 : 493)

HOLOTYPE: male. Reg. no. 1925:7:22:493. Meran. Collected by Milde. Koch Collection.

moebiusi Verhoeff (1901a : 38) [Transferred to *Porcellio lamellatus* (Ulj.) Budde-Lund]

SYNTYPES: two females. Reg. no. 1901:9:19:95–96. Dalmatia, Yugoslavia. Purchased from K. W. Verhoeff.

narentanus Verhoeff (1907a : 251)

SYNTYPE: male. Reg. no. 1907:11:4:84. Herzegowina, Yugoslavia. Purchased from K. W. Verhoeff.

naupliensis Verhoeff (1901d : 403)

SYNTYPES: one male; one female; one juvenile. Reg. no. 1901:9:19:60–61. Greece. Purchased from K. W. Verhoeff.

nicklesi Dollfus (1892b : 171)

SYNTYPE: male. Reg. no. 1921:10:18:4582. Rio Clariano, Valencia, Spain. Collected by R. Nickles. Budde-Lund Collection.

nigra Say (1818 : 432) [Transferred to *Porcellio scaber* Latr.]

SYNTYPE: fragments only (dry). Reg. no. 1973:509:1. Pennsylvania, USA. Presented by T. Say.

normani (Dollfus) (1899 : 67) [*Lucasius normani*]

SYNTYPES: one male; two females. Reg. no. 1911:11:8:10535–10537. Ilheo dos Embarcadouros, Madeira I. 1897. Collected by A. M. Norman. Norman Collection.

obsoletus Budde-Lund (1885 : 116)

SYNTYPES: three males; five females. Reg. no. 1921:10:18:5002–5007. Sebastopol, Ukraine, USSR. Budde-Lund Collection.

obtusifrons Haswell (1882 : 280) [Transferred to *Porcellio laevis* Latreille]

SYNTYPES: two females. Reg. no. 1895:11:14:38–39. Sydney, Australia. Presented by the Australian Museum, Sydney.

obtusiserra Barnard (1940 : 357)

SYNTYPES: six males; one female; one juvenile. Reg. no. 1949:2:2:118–137 (part). Addis Ababa, Ethiopia. 16.9.1926. Collected and presented by J. Omer-Cooper.

SYNTYPES: one male; one female. Reg. no. 1949:2:2:118–137 (part). Djem Djem Forest, Ethiopia. 25.9.1926. Collected and presented by J. Omer-Cooper.

SYNTYPES: nine males; twenty females. Reg. no. 1949:2:2:118–137 (part). Djem Djem Forest, Ethiopia. Pond no. 1, 8100 ft. 21.9.1926. Collected and presented by J. Omer-Cooper.

ocellatus Budde-Lund (1885 : 111)

SYNTYPES: four males; three females. Reg. no. 1921:10:18:4600–4606. Spain ('Hispania meridionalis'). Collected by L. Lund. Budde-Lund Collection.

orarum orarum Verhoeff (1910 : 139) [*Porcellio lugubris orarum*]

SYNTYPES: one male; four females. Reg. no. 1921:6:10:23–27. Riviera, France. Purchased from K. W. Verhoeff.

orarum vizzavonensis Verhoeff (1928c : 123) [*Porcellio lugubris vizzavonensis*]

HOLOTYPE: male. Reg. no. 1928:7:4:12. Vizzavona, Corsica. Purchased from K. W. Verhoeff.

parietinus L. Koch (1901 : 49) [Transferred to *Porcellio scaber* Latreille]

SYNTYPES: one male; two females. Reg. no. 1925:7:22:496–498. Landstuhl, W. Germany. Koch Collection.

parvus Budde-Lund (1885 : 132)

SYNTYPES: three females. Reg. no. 1921:10:18:5026–5027. Sicily. Collected by Grohmann. Budde-Lund Collection.

pauper Budde-Lund (1885 : 305)

SYNTYPE: specimen in fragments. Reg. no. 1921:10:18:5845. Tlemcen, Algeria. Collected by E. Simon. Budde-Lund Collection.

planarius Budde-Lund (1885 : 95)

SYNTYPE : male. Reg. no. 1921:10:18:4993. Sicily. Collected by Grohmann. Budde-Lund Collection.

praeustus Budde-Lund (1885 : 302)

SYNTYPE : male. Reg. no. 1921:10:18:4994. Bon-Merzong, Algeria. Collected by E. Simon. Budde-Lund Collection.

provincialis Aubert & Dollfus (1890 : 7)

SYNTYPE : male. Reg. No. 1911:11:8:10402. 'Galets de la Crau', Marseilles, France. Norman Collection (ex Dollfus collection).

pujetanus Verhoeff (1910 : 136) [Transferred to *Porcellio spinipennis spinipennis* Budde-Lund]

SYNTYPE : female. Reg. no. 1921:6:10:22. French Riviera. Purchased from K. W. Verhoeff.

purpureus Budde-Lund (1885 : 303)

SYNTYPE : male. Reg. no. 1911:11:8:10422. Oran, Algeria. Collected by E. Simon. Norman Collection (ex Dollfus collection).

pyrenaeus Dollfus (1892b : 175)

SYNTYPES : one female ; one juvenile. Reg. no. 1911:11:8:10407–10408. Vallée de Sallanques, Spanish Pyrenees. 1200 m. Norman Collection (ex Dollfus collection).

ragusae Dollfus (1896b : 2)

SYNTYPES : two females. Reg. no. 1911:11:8:10391–10392. Selinunte (ruins), Sicily. Norman Collection (ex Dollfus collection).

SYNTYPES : one male ; one female. Reg. no. 1921:10:18:4702–4703. Ficuzza, near Palermo, Italy. Budde-Lund Collection (ex Dollfus collection)

SYNTYPE : female. Reg. no. 1921:10:18:4711. Ficuzza, Sicily. 15.2.1889. Budde-Lund Collection.

sabulifer Verhoeff (1907a : 265)

SYNTYPE : female. Reg. no. 1907:11:4:100. Attika. Purchased from K. W. Verhoeff.

saltuum L. Koch (1901 : 45) [Transferred to *Porcellio arcuatus* Budde-Lund]

SYNTYPE : female. Reg. no. 1911:11:8:10431. Tyrol. Norman Collection (ex Koch collection).

SYNTYPES : one male ; one female. Reg. no. 1925:7:22:623–639 (part). Vahrn, Brixen, Austria. Koch Collection.

SYNTYPES : one male ; two females. Reg. no. 1925:7:22:623–638 (part). Meran, Trentino, Italy. Koch Collection.

SYNTYPES : two males ; four females. Reg. no. 1925:7:22:623–638 (part). Ratzes. Koch Collection.

SYNTYPES : one male ; two females. Reg. no. 1925:7:22:623–638 (part). Bosen, W. Germany. Koch Collection.

SYNTYPE : female. Reg. no. 1925:7:22:623–638 (part). Torbole, Italy. Koch Collection.

SYNTYPE : female. Reg. no. 1925:7:22:623–638 (part). Bayerische Alpen, W. Germany. Koch Collection.

sarajevensis Verhoeff (1907a : 255)

SYNTYPE : male. Reg. no. 1907:11:4:101. Boznya, USSR. Purchased from K. W. Verhoeff.

sarculatus Budde-Lund (1896 : 46)

SYNTYPES : fragments of two males. Reg. no. 1921:10:18:4736. Ukraine Peninsula. Budde-Lund Collection.

scaber japonicus Verhoeff (1928b : 36)

SYNTYPE : male. Reg. no. 1928:7:4:10. Hokkaido, Japan. 10.11.1904. Collected by H. Sauter. Purchased from K. W. Verhoeff.

scaber lusitanus Verhoeff (1907a : 263) [*Porcellio lusitanus*]

SYNTYPE : female. Reg. no. 1907:11:4:80. Portugal. Purchased from K. W. Verhoeff.

simulator Budde-Lund (1885 : 147)

SYNTYPES : three males ; one female. Reg. no. 1911:11:8:10418-10421. Algeria. Collected by E. Simon. Norman Collection (ex Dollfus collection).

Syntypes: one male; three females. Reg. no. 1921:10:18:4882–4886. Algeria. Collected by E. Simon. Budde-Lund Collection.

sociabilis L. Koch (1901 : 51)

Syntypes: one male; two females. Reg. no. 1911:11:8:10432–10434. Tyrol. Norman Collection (ex Koch collection).

Syntypes: ten males; eight females. Reg. no. 1925:7:22:661–670. Vahrn, Brixen, Austria. Koch Collection.

sordidus Budde-Lund (1885 : 108)

Syntype: female (?) (specimen in fragments). Reg. no. 1921:10:18:4888. Balearic Is. Collected by Schaufuss. Budde-Lund Collection.

spatulata Barnard (1940 : 357)

Syntypes: twenty-four males; thirty-eight females. Reg. no. 1949:2:2:88–117. Djem Djem Forest, Ethiopia. Pond no. 2, 8000 ft. 26.9.1926. Collected and presented by J. Omer-Cooper.

Syntypes: five males; ten females. Reg. no. 1949:2:2:88–177 (part). Djem Djem Forest, Ethiopia. Pond no. 1, 8100 ft. 21.9.1926. Collected and presented by J. Omer-Cooper.

Syntype: female. Reg. no. 1949:2:2:88–117 (part). Djem Djem Forest, Ethiopia. 22.9.1926. Collected and presented by J. Omer-Cooper.

Syntypes: three males; twelve females. Reg. no. 1949:2:2:88–117 (part). Djem Djem Forest, Ethiopia. 25.9.1926. Collected and presented by J. Omer-Cooper.

spinicornis Say (1818 : 431)

Syntypes: two males. Reg. no. 1973:508:2. North America. Presented by T. Say.

spinipennis montanus Budde-Lund (1885 : 121) [*Porcellio montanus*]

Syntypes: one male; four (?) females (specimens in fragments). Reg. no. 1921:10:18:4503–4506. France. Collected by E. Simon. Budde-Lund Collection.

spinipennis spinipennis Budde-Lund (1885 : 732) [*Porcellio spinipennis*]

Syntypes: two females. Reg. no. 1921:10:18:4889–4890. Menton, France. Collected by E. Simon. Budde-Lund Collection.

spinipes Dollfus (1893 : 53)

Syntype: male. Reg. no. 1921:10:18:4892. Canary Is. Collected by C. Alluaud. Budde-Lund Collection.

spretus Budde-Lund (1885 : 89)

Syntype: female. Reg. no. 1921:10:18:4891. Sicily. Collected by Grohmann. Budde-Lund Collection.

succinctus Budde-Lund (1885 : 304)

Syntype: female. Reg. no. 1911:11:8:10364. Carthagena, Spain. May 1883. Collected by E. Simon. Norman Collection (ex Dollfus collection).

Syntypes: one male; two females. Reg. no. 1921:10:18:4893–4895. Carthagena, Spain. May 1883. Collected by E. Simon. Budde-Lund Collection.

trachealis Budde-Lund (1885 : 90)

Syntype: female. Reg. no. 1921:10:18:4896. Moldavia. Collected by Jelski. Budde-Lund Collection.

transmutatus Budde-Lund (1885 : 122)

Syntypes: four males; one female. Reg. no. 1911:11:8:10436–10440. Algeria. Collected by Fr. Meinert. Norman Collection.

Syntypes: five males; twelve females. Reg. no. 1921:10:18:3924–3940. Algeria. Budde-Lund Collection.

trilobatus Stein (1859 : 260)

Syntype: male. Reg. no. 1921:10:18:4947. Mehadia, Roumania. Budde-Lund Collection (ex Stein collection).

Syntypes: one male; one female. Reg. no. 1925:7:22:672–675 (part). Mehadia, Roumania. Koch Collection (ex Stein collection).

vespertilio Budde-Lund (1896 : 46)

Syntype: female. Reg. no. 1921:10:18:4954. Dalmatia, Yugoslavia. Budde-Lund Collection.

violaceus Budde-Lund (1885 : 117)

SYNTYPE : female. Reg. no. 1921:10:18:4952–4953 (part). Murviedro, Spain. Collected by Collin. Budde-Lund Collection.

yemenensis Barnard (1941 : 57)

SYNTYPE : juvenile. Reg. no. 1949:2:2:1–25 (part). Western Aden Protectorate : Dhala. 4800 ft, in detritus under succulent plants. 14.9.1937. Collected by H. Scott. British Museum Expedition to S.W. Arabia, 1937–38.

SYNTYPES : two males ; one female. Reg. no. 1949:2:2:1–25 (part). Yemen : Jebel Masnah, S.W. of Ma'bar. c. 8400 ft. 9.3.1938. Collected by H. Scott and E. B. Britton. British Museum Expedition to S.W. Arabia, 1937–38.

SYNTYPES : four males ; one female. Reg. no. 1949:2:2:1–25 (part). Western Aden Protectorate : Jebel Jihaf. From summit, 7800 ft, under stones. 20.9.1937. Collected by H. Scott. British Museum Expedition to S.W. Arabia, 1937–38.

SYNTYPES : one male ; two females. Reg. no. 1949:2:2:1–25 (part). Yemen : Ghaiman. 13 miles S.E. of San'a, c. 8500 ft, found in valley near streams. 17.2.1938. Collected by H. Scott. British Museum Expedition to S.W. Arabia, 1937–38.

SYNTYPES : five females. Reg. no. 1949:2:2:1–25 (part). Yemen : Birkat al Bu'r, near Haz. About 16 miles N.W. of San'a, 9200 ft. 4.2.1938. Collected by E. B. Britton. British Museum Expedition to S.W. Arabia, 1937–38.

SYNTYPES : two males ; four females ; three juveniles. Reg. no. 1949:2:2:1–25 (part). Yemen : top of Al Errein, near Haz. 9300 ft. 3.2.1938. British Museum Expedition to S.W. Arabia, 1937–38.

SYNTYPES : two males ; two females. Reg. no. 1949:2:2:1–25 (part). Yemen : top of pass over Jebel Sumara. 9200–9700 ft. 2–3.1.1938. Collected by E. B. Britton. British Museum Expedition to S.W. Arabia, 1937–38.

zealandicus Miers (1876 : 226) [Transferred to *Metoponorthus pruinosus* Brandt]

HOLOTYPE : female (dry). Reg. no. 1845:30. New Zealand. Purchased from Mr Earl.

PORCELLIONIDES Miers

dimorphus Jackson (1926 : 186)

SYNTYPES : three males ; three females. Reg. no. 1925:10:14:28–32. Mont Estoril, near Lisbon, Portugal. Collected and presented by E. R. Speyer.

SYNTYPES : two males ; five females. Reg. no. 1952:4:18:153–159. Mont Estoril, near Lisbon, Portugal. Collected by E. R. Speyer. Jackson Collection.

variabilis Jackson (1926 : 187)

SYNTYPES : four males ; twelve females. Reg. no. 1925:10:14:34–43. Mont Estoril, nr. Lisbon, Portugal. February 1925. Collected and presented by E. R. Speyer.

SYNTYPES : two males ; eleven females. Reg. no. 1952:4:18:160–169. Mont Estoril, near Lisbon, Portugal. February 1925. Collected by E. R. Speyer. Jackson Collection.

TURA Budde-Lund

albipennis Budde-Lund (1913b : 379)

SYNTYPES : two males. Reg. no. 1921:10:18:3983–3984. Ethiopia. Collected by E. Wache. Budde-Lund Collection.

angusta Budde-Lund (1913b : 378)

SYNTYPES : one male ; nine females. Reg. no. 1921:10:18:3985–3994. Aldabra I., Indian Ocean. Collected by H. P. Thomasset. Budde-Lund Collection.

laticauda Budde-Lund (1913b : 379)

SYNTYPE : male. Reg. no. 1921:10:18:3995. Ethiopia. Budde-Lund Collection.

testacea Budde-Lund (1908 : 282)

SYNTYPES : six males ; seventeen females. Reg. no. 1921:10:18:3996–4007. Majunga, Madagascar. 1894. Collected by A. Voeltzkow. Budde-Lund Collection.

URAMBA Budde-Lund

marginalis Budde-Lund (1910 : 19)

SYNTYPES : six males ; three females. Reg. no. 1921:10:18:4070–4078. Tanganyika : Kibonoto, Kilimanjaro ; Ngara na nyuki, Meru, in acacia forest. January 1906. Budde-Lund Collection.

mus (Budde-Lund) (1898 : 9) [*Lyprobius mus*]

SYNTYPES : one male ; one specimen in fragments. Reg. no. 1921:10:18:4079–4080. Zanzibar I., East Africa. Collected by A. Voeltzkow. Budde-Lund Collection.

triangulifera Budde-Lund (1910 : 18)

SYNTYPES : three males ; seven females. Reg. no. 1921:10:18:4085–4094. Kilimanjaro, Tanganyika. Budde-Lund Collection.

Family BALLONISCIDAE

BALLONISCUS Budde-Lund

maculata (Budde-Lund) (1885 : 215) [*Philoscia maculata*]

SYNTYPES : three females. Reg. no. 1921:10:18:1708–1710. Buenos Aires (probably San Nicolas), Agentina. Collected by W. Sørensen. Budde-Lund Collection.

PLATAONISCUS Vandel

borelli (Dollfus) (1897 : 3) [*Alloniscus borellii*]

SYNTYPE : male. Reg. no. 1921:10:18:1701. San Lorenzo, Jujuy, Argentina. Collected by A. Borelli. Budde-Lund Collection.

SYNTYPE : male. Reg. no. 1956:10:10:151. San Lorenzo, Jujuy, Argentina. Collected by A. Borelli. Presented by University College, Dundee.

Family TRACHELIPIDAE

AGNARA Budde-Lund

fragilis Budde-Lund (1908 : 287)

SYNTYPES : three males ; one female. Reg. no. 1921:10:18:5551–5554. Ceylon. January 1904. Collected by K. Kraepelin. Budde-Lund Collection.

madagascariensis (Budde-Lund) (1885 : 189) [*Metoponorthus madagascariensis*]

SYNTYPES : two males ; one female. Reg. no. 1921:10:18:5556–5558. Madagascar. Collected by Hildebrandt. Budde-Lund Collection.

NAGURUS Holthius

formosanus (Verhoeff) (1928a : 214) [*Nagara formosana*]

SYNTYPE : male. Reg. no. 1928:7:4:7. Taiwan I. Purchased from K. W. Verhoeff.

incisus (Verhoeff) (1928a : 215) [*Nagara incisa*]

SYNTYPE : female. Reg. no. 1928:7:4:8. Taiwan I. Purchased from K. W. Verhoeff.

nanus (Budde-Lund) (1908 : 285) [*Nagara nana*]

SYNTYPES : six males ; seven females. Reg. no. 1921:10:18:1495–1506. Madagascar. Budde-Lund Collection.

travancorius (Verhoeff) (1936b : 100) [*Nagara travancoria*]

SYNTYPES : two females. Reg. no. 1938:7:7:22–23. Deccan, India. Purchased from K. W. Verhoeff.

ORTHOMETOPON Verhoeff

dalmatinus frascatensis Verhoeff (1918 : 147)

SYNTYPES : one male ; one female. Reg. no. 1921:6:10:33-34. S. Italy. Purchased from K. W. Verhoeff.

phaleronensis (Verhoeff) (1901d : 407) [*Porcellio* (*Metoponorthus*) *phaleronensis*]

SYNTYPES : two females. Reg. no. 1901:9:19:42-43. Phaleron, Greece. Purchased from K. W. Verhoeff.

PAGANA Budde-Lund

fissifrons Budde-Lund (1908 : 289)

SYNTYPES : one male ; two females. Reg. no. 1921:10:18:5547-5548. Mauritius I., Indian Ocean. Budde-Lund Collection.

maculosa Budde-Lund (1908 : 288)

SYNTYPES : two females. Reg. no. 1921:10:18:5549-5550. Mauritius I., Indian Ocean. Budde-Lund Collection.

PHALABA Budde-Lund

brevis Budde-Lund (1910 : 19)

SYNTYPES : two males ; twelve females. Reg. no. 1921:10:18:2091-2103. Kibonoto, Kilimanjaro, Tanganyika. Budde-Lund Collection.

PORCELLIUM Dahl

collicolus (Verhoeff) (1907a : 247) [*Porcellio* (*Porcellidium*) *collicolus*]

SYNTYPE : male. Reg. no. 1907:11:4:65. W. Hungary. Purchased from K. W. Verhoeff.

herzegovinensis (Verhoeff) (1901b : 69) [*Porcellio herzegovinensis*]

SYNTYPES : one male ; two females. Reg. no. 1901:9:19:90-92. Herzegovina, Yugoslavia. Purchased from K. W. Verhoeff.

PROTRACHEONISCUS Verhoeff

desertorum Verhoeff (1930b : 112)

SYNTYPE : female. Reg. no. 1930:5:26:71. Tashkent, Uzbekistan, USSR. Purchased from K. W. Verhoeff.

fontium Verhoeff (1930b : 112)

SYNTYPES : one female ; four juveniles. Reg. no. 1930:5:26:65-69. Turkestan, USSR. Purchased from K. W. Verhoeff.

hermagorensis Verhoeff (1927 : 327)

SYNTYPE : female. Reg. no. 1931:4:27:47. Karnten, Austria. Purchased from K. W. Verhoeff.

hirsutulus Verhoeff (1930b : 115)

SYNTYPE : female. Reg. no. 1930:5:26:70. Tashkent, Uzbekistan, USSR. Purchased from K. W. Verhoeff.

latus Verhoeff (1930b : 110)

SYNTYPES : two females. Reg. no. 1930:5:26:63-64. Turkestan, USSR. Purchased from K. W. Verhoeff.

SYNTYPES : two males ; two females. Reg. no. 1938:7:7:26-29. Turkestan, USSR. Purchased from K. W. Verhoeff.

politus mehelyi Kesselyák (1930 : 250) [*Protracheoniscus mehelyi*]

SYNTYPE : female. Reg. no. 1931:4:27:48. Monte Maggiore, Italy. Purchased from K. W. Verhoeff.

saxonicus Verhoeff (1927 : 324)

SYNTYPES : one male ; one female. Reg. no. 1928:7:4:50–51. Bayern, W. Germany. Purchased from K. W. Verhoeff.

saxonicus carpathicus Verhoeff (1928c : 52)

SYNTYPE : female. Reg. no. 1928:7:4:52. Carpathian Mts, Central Europe. Purchased from K. W. Verhoeff.

taschkententis Verhoeff (1930b : 113)

SYNTYPE : female. Reg. no. 1930:5:26:72. Turkestan, USSR. Purchased from K. W. Verhoeff.

venetus Verhoeff (1927 : 328)

SYNTYPES : one male ; one female. Reg. no. 1928:7:4:53–54. Veneto region, Italy. Purchased from K. W. Verhoeff.

TRACHELIPUS Budde-Lund

apenninorum (Verhoeff) (1931a : 538) [*Tracheoniscus apenninorum*]

SYNTYPE : female. Reg. no. 1931:4:27:57. Umbria, Italy. Purchased from K. W. Verhoeff.

SYNTYPES : three males ; one female. Reg. no. 1937:7:6:35–38. Apennine Mts, Italy. Purchased from K. W. Verhoeff.

apulicus (Verhoeff) (1939 : 215) [*Tracheoniscus apulicus*]

SYNTYPES : one male ; one female. Reg. no. 1938:7:7:16–17. Apulia, Italy. Purchased from K. W. Verhoeff.

balticus (Verhoeff) (1907a : 258) [*Porcellio balticus*]

SYNTYPE : female. Reg. no. 1907:11:4:63. Brandenburg, E. Germany. Purchased from K. W. Verhoeff.

balticus burzenlandicus (Verhoeff) (1907a : 258) [*Porcellio balticus burzenlandicus*]

SYNTYPE : female. Reg. no. 1907:11:4:64. Siebenbürgen, Germany. Purchased from K. W. Verhoeff.

brentanus (Verhoeff) (1927 : 332) [*Tracheoniscus brentanus*]

SYNTYPE : female. Reg. no. 1928:7:4:95. Venezia province, Italy. Purchased from K. W. Verhoeff.

bulgaricus (Verhoeff) (1926a : 143) [*Tracheoniscus bulgaricus*]

SYNTYPE : male. Reg. no. 1928:7:4:93. Bulgaria. Collected by I. Buresch. Purchased from K. W. Verhoeff.

larii (Verhoeff) (1927 : 331) [*Tracheoniscus larii*]

SYNTYPE : male. Reg. no. 1928:7:4:94. Lake Como, Italy. Purchased from K. W. Verhoeff.

larii aternanus (Verhoeff) (1931a : 539) [*Tracheoniscus larii aternanus*]

SYNTYPE : female. Reg. no. 1931:4:27:53. L'Aquila, Abruzzi, Italy. Purchased from K. W. Verhoeff.

lutshniki (Verhoeff) (1933 : 107) [*Tracheoniscus lutshniki*]

SYNTYPES : two females. Reg. no. 1938:7:7:20–21. Sotshi, N. Caucasus Mts. July 1931. Collected by V. Lutshnik. Purchased from K. W. Verhoeff.

phaeacorum (Verhoeff) (1901b : 71) [*Porcellio rathkei phaeacorum*]

SYNTYPE : male. Reg. no. 1901:9:19:64. Korfu I., Greece. Purchased from K. W. Verhoeff.

SYNTYPE : male. Reg. no. 1907:11:4:85. Korfu I., Greece. Purchased from K. W. Verhoeff.

pseudoratzeburgi (Verhoeff) (1907a : 259) [*Porcellio* (*Euporcellio*) *pseudoratzeburgi*]

SYNTYPE : female. Reg. no. 1907:11:4:87. Boznya, USSR. Purchased from K. W. Verhoeff.

Family **ARMADILLIDIIDAE**

ARMADILLIDIUM Brandt

aegaeum Strouhal (1929 : 102)

SYNTYPE : female. Reg. no. 1931:4:27:32. Skyros I. May 1927. Collected by F. Werner. Purchased from K. W. Verhoeff.

alassiense Verhoeff (1910 : 121)

SYNTYPES : four females. Reg. no. 1937:7:6:6–9. Italian Riviera. Purchased from K. W. Verhoeff.

albanicum Verhoeff (1901a : 37)

SYNTYPES : two females. Reg. no. 1901:9:19:15–16. Korfu I., Greece. Purchased from K. W. Verhoeff.

SYNTYPE : male. Reg. no. 1921:10:18:2622. Aulaona, Albania. Collected by Oertzen. Budde-Lund Collection.

albifrons L. Koch (1901 : 25)

SYNTYPE : female. Reg. no. 1925:7:22:207. Merano, Italy. Collected by Milde. Koch Collection.

album Dollfus (1887 : 4)

SYNTYPE : female. Reg. no. 1921:10:18:2623. Arcachon, France. Budde-Lund Collection.

anconanum Verhoeff (1928c : 98)

SYNTYPES : two males ; one female. Reg. no. 1928:7:4:97–99. Ancona, Italy. Purchased from K. W. Verhoeff.

apenninorum Verhoeff (1928c : 109)

SYNTYPE : male. Reg. no. 1928:7:4:103. Ancona, Italy. Purchased from K. W. Verhoeff.

apfelbecki Dollfus (1896d : 584)

SYNTYPE : female. Reg. no. 1901:9:19:31. Herzegovina, Yugoslavia. Purchased from K. W. Verhoeff.

SYNTYPES : two females. Reg. no. 1911:11:8:9956–9957. Stolac, Yugoslavia. Norman Collection.

argentarium Verhoeff (1931a : 518)

SYNTYPES : two females. Reg. no. 1931:4:27:39–40. Monte Argentario, Italy. Purchased from K. W. Verhoeff.

SYNTYPE : female. Reg. no. 1970:76:1. Monte Argentario, Italy. Larwood Collection (ex Verhoeff collection).

astriger (C. L. Koch) (1841 : 4) [*Armadillo astriger*]

SYNTYPE (?) : one female. Reg. no. 1925:7:22:208. Dalmatia, Yugoslavia. Koch Collection.

badium Budde-Lund (1885 : 60)

SYNTYPES : two males ; one female. Reg. no. 1921:10:18:2661–2663. Egypt. Collected by Fischer. Budde-Lund Collection.

badium siculorum Verhoeff (1908c : 491)

SYNTYPES : two males ; two females. Reg. no. 1921:6:10:14–17. Palermo region, Sicily. Purchased from K. W. Verhoeff.

caelatum Miers (1877b : 665)

SYNTYPES : two males ; one female. Reg. no. 1879:21. Cayenne, Guiana. Presented by Prof. A. Wrzésniowsky.

carniolense Verhoeff (1901b : 67)

SYNTYPES : one male ; one female ; one juvenile. Reg. no. 1928:7:4:100–102. Adelsberg, Krain (Carniola), Austria. Purchased from K. W. Verhoeff.

cingendum Verhoeff (1910 : 119) [*Armadillidium maculatum cingendum*]

SYNTYPES : one male ; two females. Reg. no. 1921:6:10:11–13. Italian Riviera. Purchased from K. W. Verhoeff.

Syntype : male. Reg. no. 1970:32:1. Italian Riviera. Larwood Collection (ex Verhoeff collection).

corcyraeum Verhoeff (1901b : 68)

Syntypes : two males. Reg. no. 1901:9:19:18–19. Corfu I., Greece. Purchased from K. W. Verhoeff.

Syntype : specimen in fragments. Reg. no. 1921:10:18:2713. Corfu I., Greece. Budde-Lund Collection.

davidi Dollfus (1887 : 4)

Syntype : female. Reg. no. 1911:11:8:9930. Syria. Collected by Abbé David. Norman Collection.

elbanum Verhoeff (1931a : 522) [Transferred to *Armadillidium assimile* Budde-Lund]

Syntypes : one male ; one juvenile ; one specimen with genitalia missing. Reg. no. 1931:4:27:36–37. Elba. Purchased from K. W. Verhoeff.

Syntypes : one male ; one female. Reg. no. 1970:77:2. Elba. Larwood Collection (ex Verhoeff collection).

esterelanum Dollfus (1887 : 2)

Syntype : female. Reg. no. 1892:12:6:4. Estérel, France. Presented by W. D'Arcy Thompson.

Syntype : female. Reg. no. 1911:11:8:9980. Mt Vinaigre, Estérel Mts, France. Norman Collection.

Syntypes : two males ; two females. Reg. no. 1921:10:18:2839–2841. Estérel Mts, France. Budde-Lund Collection.

Syntypes : one male ; one female. Reg. no. 1921:12:1:1422–1423. Estérel Mts, France. Stebbing Collection.

Syntype : female. Reg. no. 1956:10:10:181. Estérel Mts, France. Presented by University College, Dundee.

flavoscutatum Strouhal (1927 : 28)

Syntype : female. Reg. no. 1928:7:4:115. Shkodër (formerly Skutari), Albania. Purchased from K. W. Verhoeff.

frontexcavatum Verhoeff (1931a : 517)

Syntype : male. Reg. no. 1931:4:27:35. Umbria, Italy. Purchased from K. W. Verhoeff.

Syntype : male. Reg. no. 1970:78:1. Umbria, Italy. Larwood Collection (ex Verhoeff collection).

frontirostre Budde-Lund (1885 : 52)

Syntypes : one male ; two females ; one juvenile. Reg. no. 1921:10:18:2863–2866. Italy. Collected by J. Collin. Budde-Lund Collection.

furcatum Budde-Lund (1885 : 72)

Syntypes : one male ; one female. Reg. no. 1921:10:18:2885–2886. Rome, Italy. Budde-Lund Collection.

gestroi Tua (1900 : 5)

Syntypes : six males ; six females. Reg. no. 1921:10:18:2887–2898. Finalmarina. Collected by R. Gestro. Budde-Lund Collection.

graecorum Verhoeff (1907b : 474)

Syntype : male. Reg. no. 1907:11:4:2. Mid-Greece. Purchased from K. W. Verhoeff.

grandinatum Budde-Lund (1885 : 58)

Syntypes : one male ; one female. Reg. no. 1921:10:18:2899–2900. Sicily. Collected by Grohmann. Budde-Lund Collection.

granulatum peloponnesiaca Verhoeff (1901c : 139)

Syntype : female. Reg. no. 1901:9:19:1. Návplion, Greece. Purchased from K. W. Verhoeff.

hirtum Budde-Lund (1885 : 64)

Syntypes : one male ; one female. Reg. no. 1921:10:18:2944–2945. Sicily. Collected by Grohmann. Budde-Lund Collection.

laminigerum Verhoeff (1907b : 481)

Syntype : male. Reg. no. 1907:11:4:4. Middle Greece. Purchased from K. W. Verhoeff.

mareoticum Budde-Lund (1885 : 59)

Syntype : female. Reg. no. 1921:10:18:2992. Egypt. Collected by Fischer. Budde-Lund Collection.

marinensium Verhoeff (1928c : 105)

Syntype : female. Reg. no. 1928:7:4:116. San Marino Republic, Italy. Purchased from K. W. Verhoeff.

mohamedanicum Verhoeff (1929 : 131)

Syntype : female. Reg. no. 1928:7:4:104. Kuru Dag Mt, Gelibolu, Thrace region, Turkey. Collected by I. Buresch. Purchased from K. W. Verhoeff.

muricatum Budde-Lund (1885 : 297)

Syntypes : two males ; eleven females. (This includes unregistered specimens collected by Ehlers in 1879, which are in the same tube.) Reg. no. 1921:10:18:3038–3042. Cartagena, Spain. Collected by E. Simon. Budde-Lund Collection.

Syntype : female. Reg. no. 1911:11:8:9958–9959. Cartagena, Spain. Collected by E. Simon. Norman Collection.

nasatum sorrentinum Verhoeff (1908c : 487)

Syntypes : one male ; four females. Reg. no. 1921:6:10:4–9. Southern Italy. Purchased from K. W. Verhoeff.

nitidulus Collinge (1915b : 463) [Transferred to *Armadillidium vulgare* (Latreille)]

Syntype : female. Reg. no. 1919:4:26:503. Madeira, Spain. Collected by J. W. Clark. Collinge Collection.

odherni Verhoeff (1930c : 45) [*Armadillidium peraccai odherni*]

Syntypes : two males ; two females. Reg. no. 1930:5:26:6–11. Dalmatia. Purchased from K. W. Verhoeff.

Syntypes : three males ; four females. Reg. no. 1937:7:6:1–5. Yugoslavia. Purchased from K. W. Verhoeff.

oliveti L. Koch (1901 : 31) [Transferred to *Armadillidium vulgare* (Latreille)]

Syntypes : two males. Reg. no. 1911:11:8:9998–9999. Tirol, Austria. Norman Collection.

Syntypes : five males ; nine females. Reg. no. 1925:7:22:281–297 (part). Nago, nr. Torbole, Italy. Koch Collection.

Syntypes : two males ; one female. Reg. no. 1925:7:22:281–297 (part). Bozen. Koch Collection.

ormeanum Verhoeff (1931a : 521)

Syntype : female. Reg. no. 1930:5:6:24. Liguria, Italy. Purchased from K. W. Verhoeff.

Syntype : female. Reg. no. 1970:68:1. Liguria, Italy. Larwood Collection (ex Verhoeff collection).

pellegrinense Verhoeff (1908c : 456) [Transferred to *Armadillidium granulatum* Brandt].

Syntype : male. Reg. no. 1921:6:10:8. Sicily. Purchased from K. W. Verhoeff.

peraccae Tua (1900 : 2) [Transferred to *Armadillidium pallasi* Brandt]

Syntypes : two males ; two females. Reg. no. 1911:11:9:9940–9943. Otranto, Italy. Collected by Peracca. Norman Collection.

petraeum L. Koch (1901 : 26)

Syntypes : two males. Reg. no. 1911:11:8:9996–9997. Tirol, Austria. Norman Collection.

Syntypes : eight males ; seven females. Reg. no. 1925:7:22:311–325. Torbole, Italy. Koch Collection.

portofinense Verhoeff (1908c : 459)

Syntype : female. Reg. no. 1907:11:4:21. Portofino, Italian Riviera. Purchased from K. W. Verhoeff.

SYNTYPES: one male; three females. Reg. no. 1970:42:6. Portofino, Italian Riviera. Larwood Collection (ex Verhoeff collection).

pujetanum Verhoeff (1910 : 118). [Transferred to *Armadillidium simoni* Dollfus]

SYNTYPE: female. Reg. no. 1921:6:10:10. Riviera. Purchased from K. W. Verhoeff.

quadriserriatum Verhoeff (1908c : 457)

SYNTYPES: one male; three females. Reg. no. 1907:11:4:23–26. Noli, Italian Riviera. Purchased from K. W. Verhoeff.

SYNTYPE: male. Reg. no. 1970:43:1. Noli, Italian Riviera. Larwood Collection (ex Verhoeff collection).

quinquepustulatum Budde-Lund (1885 : 294)

SYNTYPES: two males. Reg. no. 1921:10:18:3183–3184. Ouled Anteurs, Algeria. Collected by E. Simon. Budde-Lund Collection.

rehobotense Verhoeff (1917 : 172)

SYNTYPES: two males; one female. Reg. no. 1921:6:10:19–20. Jaffa, Israel. Collected by Aharoni. Purchased from K. W. Verhoeff.

riparium L. Koch (1901 : 28)

SYNTYPES: one male; one female. Reg. no. 1925:7:22:374–375. Torbole, Italy. Koch Collection.

rosai Arcangeli (1913 : 184)

SYNTYPE: female. Reg. no. 1931:4:27:33. Bergamask Alpen, Bergamo, Italy. Purchased from K. W. Verhoeff.

sanctum Dollfus (1892c : 4)

SYNTYPE: female. Reg. no. 1911:11:8:9979. Ramlah, Syria. Collected by Letourneux. Norman Collection.

SYNTYPES: one male; three females. Reg. no. 1921:10:18:5850–5853. Ramlah, Syria. Collected by Letourneux. Budde-Lund Collection.

savonense Verhoeff (1931a : 520)

SYNTYPE: female. Reg. no. 1930:5:6:23. Savona, Italy. Purchased from K. W. Verhoeff.

scaberrimum Stein (1859 : 264)

SYNTYPE: male. Reg. no. 1921:10:18:3228. Dubrovnik (Ragusa), Yugoslavia. Budde-Lund Collection.

scabrum Dollfus (1892b : 165)

SYNTYPES: one male; one female. Reg. no. 1911:11:8:9991–9992. Constantina, Spain. Collected by Calderón. Norman Collection.

serratum Budde-Lund (1885 : 297)

SYNTYPES: one male; one female. Reg. no. 1921:10:18:3239–3240. La Preste, central France. Collected by E. Simon. Budde-Lund Collection.

simoni Dollfus (1887 : 2)

SYNTYPE: male. Reg. no. 1892:12:6:3. Cannes, France. Presented by W. D'Arcy Thompson.

SYNTYPES: three females. Reg. no. 1911:11:8:9963–9965. Cannes, France. 'Pine forest, under stones.' Norman Collection.

SYNTYPES: three males; one female. Reg. no. 1921:10:18:3249–3252. Cannes, France. Budde-Lund Collection (ex Dollfus collection).

SYNTYPES: two females. Reg. no. 1928:12:1:1455–1457 (part). Cannes, France. Stebbing Collection (ex Dollfus collection).

SYNTYPE: male. Reg. no. 1956:10:10:198. Cannes, France. Presented by University College, Dundee.

simoni gigas Verhoeff (1931a : 519)

SYNTYPE: female. Reg. no. 1931:4:27:38. Toscana, Italy. Purchased from K. W. Verhoeff.

SYNTYPE: female. Reg. no. 1970:69:1. Monte Pisani, Italy. Larwood Collection (ex Verhoeff collection).

speyeri Jackson (1923 : 224) [Transferred to *Armadillidium nasatum* Budde-Lund]

HOLOTYPE: male. Reg. no. 1924:5:15:1. Cheshunt, Hertfordshire, England. 'In the cucumber houses of the Experimental and Research Station.' Collected and presented by E. Speyer.

PARATYPES: six males; eleven females. Reg. no. 1924:5:15:2–11. Cheshunt, Hertfordshire, England. Collected and donated by E. Speyer.

PARATYPES: twenty-one juveniles. Reg. no. 1952:4:18:231–235. Cheshunt, Hertfordshire, England. Collected by E. Speyer. Jackson Collection.

stolikanum Verhoeff (1907b : 469)

SYNTYPE: female. Reg. no. 1907:11:4:22. Stoliko, Middle Greece. Purchased from K. W. Verhoeff.

subdentatum Haswell (1882 : 279) [Redetermined by Budde-Lund as *Armadillidium vulgare* (Latreille)]

SYNTYPE: male. Reg. no. 1895:11:14:87–88 (part). Tasmania, Australia. Presented by the Australian Museum, Sydney.

tendanum Verhoeff (1931a : 522) [Transferred to *Armadillidium alassiense* Verhoeff]

SYNTYPE: female. Reg. no. 1930:5:6:25. Tenda, Italy. Purchased from K. W. Verhoeff.

SYNTYPES: one male; two females. Reg. no. 1937:7:6:10–12. Tenda, Italy. Purchased from K. W. Verhoeff.

SYNTYPE: male. Reg. no. 1970:71:1. Tenda, Italy. Larwood Collection (ex Verhoeff collection).

tigris Budde-Lund (1885 : 55)

SYNTYPE: male. Reg. no. 1921:10:18:3304. Madeira I. Collected by Metschnikoff. Budde-Lund Collection.

tirolense Verhoeff (1901b : 67)

SYNTYPES: one male; four females. Reg. no. 1901:9:19:10–14. Southern Tirol, Austria. Purchased from K. W. Verhoeff.

tunetanum Verhoeff (1907b : 473)

SYNTYPE: female. Reg. no. 1907:11:4:30. Tunis, Tunisian Republic, N. Africa. Purchased from K. W. Verhoeff.

vallombrosae Verhoeff (1907b : 480)

SYNTYPES: five females. Reg. no. 1937:7:6:21–25. Vallombrosa, Apennines, Italy. Purchased from K. W. Verhoeff.

versicolor Stein (1859 : 265)

SYNTYPE: female. Reg. no. 1921:10:18:3350. Dubrovnik (formerly Ragusa), Yugoslavia. Budde-Lund Collection.

ELUMA Budde-Lund

purpurascens Budde-Lund (1885 : 48)

SYNTYPES: three females; one juvenile. Reg. no. 1921:10:18:3769–3772. Madeira I. Collected by Metschnikoff. Budde-Lund Collection.

EXZAES Barnard

bicolor Barnard (1932 : 300)

SYNTYPES: fifty females; two juveniles. Reg. no. 1933:1:25:292–301. Oudebosch Forest, River Zonder End Mts, Cape Province, South Africa. Collected by K. H. Barnard. Presented by the South African Museum.

sylvatica Barnard (1932 : 299)

SYNTYPES: two females. Reg. no. 1933:1:25:287–291. George Forest, Cape Province, South Africa. Collected by K. H. Barnard. Presented by the South African Museum.

HEKELUS Barnard

episimus Barnard (1932 : 298)

SYNTYPES : three males ; fourteen females ; thirteen juveniles. Reg. no. 1933:1:25:278–286. Table Mts and Noordhoek Forest, Cape Peninsula, South Africa. Collected by K. H. Barnard. Presented by the South African Museum.

PARELUMA Omer-Cooper

minuta Omer-Cooper (1923 : 396)

SYNTYPES : two females. Reg. no. 1922:5:18:11–12. Amarah, Iraq. 13.11.1918. Collected by W. E. Evans. Presented by J. Omer-Cooper.

SCHIZIDIUM Verhoeff

hybridum (Budde-Lund) (1896 : 44) [*Armadillidium hybridum*]

HOLOTYPE : fragment only. Reg. no. 1921:10:18:2960. Symi, Greece. 7.6.1887. Collected by E. von Oertzen. Budde-Lund Collection.

oertzeni (Budde-Lund) 1896 : 42 [*Armardillidium oertzeni*]

SYNTYPES : one male ; five females. Reg. no. 1921:10:18:3086–3091. Karpathos (May 1887) and Rhodos, Greece. Collected by E. von Oertzen. Budde-Lund Collection.

SUNNIVA Budde-Lund

mammillata Barnard (1936 : 8)

SYNTYPES : one male ; two females. Reg. no. 1936:7:13:43–44. Le Pouce, Mauritius I., 2400 ft. 10.1.1935. Collected and presented by R. F. Lawrence, Natal Museum.

minor Budde-Lund (1908 : 268)

SYNTYPE : few fragments only. Reg. no. 1921:10:18:937. Mauritius I. Collected by A. Voeltzkow. Budde-Lund Collection.

mystica Budde-Lund (1908 : 267)

SYNTYPE : few fragments only. Reg. no. 1921:10:18:938. Madagascar I. Collected by A. Voeltzkow. Budde-Lund Collection.

uniformis Barnard (1936 : 9)

SYNTYPES : five males ; six females. Reg. no. 1936:7:13:45–49. Le Pouce, Mauritius I., 2400 ft. 10.1.1935. Collected and presented by R. F. Lawrence, Natal Museum.

Family **EUBELIDAE**

BENECHINUS Budde-Lund

armatus Budde-Lund (1910 : 4)

SYNTYPES : two males ; four females. Reg. no. 1921:10:18:772–777. Meru Mt, Tanganyika, 3000–3500 m. Budde-Lund Collection.

ETHELUM Budde-Lund

americanum (Dollfus) (1896c : 397) [*Mesarmadillo americanus*]

SYNTYPE : female. Reg. no. 1896:1:11:20. Leeward Is., West Indies. ‘Lowland near sea. May. Under stones.’ Collected by H. H. Smith. Presented by the West India Committee.

SYNTYPES : four females. Reg. no. 1896:1:11:21. St Vincent, West Indies. ‘Sugar cane field. March. Under decaying cane leaves.’ Collected by H. H. Smith. Presented by the West India Committee.

SYNTYPES: four females. Reg. no. 1896:1:11:22. St Vincent, West Indies. 'Shady place. 259 ft. Under old boards. September.' Collected by H. H. Smith. Presented by the West India Committee.

SYNTYPES: one male; one female; one juvenile. Reg. no. 1896:1:11:23. Leeward Is., West Indies. '500 ft. March. Under rubbish, shady place.' Collected by H. H. Smith. Presented by the West India Committee.

SYNTYPE: female. Reg. no. 1921:10:18:771. St Vincent, West Indies. Collected by H. H. Smith. Budde-Lund Collection.

modestum (Dollfus) (1896c : 397) [*Mesarmadillo modestus*]

HOLOTYPE (?): female. Reg. no. 1896:1:11:24. St Vincent, West Indies. 'Low ground S.E. of the Island, under rubbish.' Collected by H. H. Smith. Presented by the West India Committee.

reflexum (Dollfus) (1896c : 398) [*Mesarmadillo reflexus*]

HOLOTYPE: female. Reg. no. 1896:1:11:19. St Vincent, West Indies. 'Open swampy land, southern end of Island. 27 September. Under rubbish.' Collected by H. H. Smith. Presented by the West India Committee.

EUBELUM Budde-Lund

dollfusi Budde-Lund (1899 : 8)

SYNTYPE: female. Reg. no. 1921:10:18:589. Antoto, Shoa district, Ethiopia. August 1885. Collected by V. Ragazzi. Budde-Lund Collection.

ignavum Budde-Lund (1899 : 9)

SYNTYPE: fragments only. Reg. no. 1921:10:18:590. Let-Marfia, Shoa district, Ethiopia. March 1885. Collected by V. Ragazzi. Budde-Lund Collection.

instrenuum Budde-Lund (1912c : 2)

SYNTYPES: one male; ten females. Reg. no. 1921:10:18:597–607. Escarpment, East Africa. Collected by E. Lonnberg. Budde-Lund Collection.

lubricum Budde-Lund (1885 : 292)

SYNTYPES: four males; three females. Reg. no. 1921:10:18:619–625. Landana, Angola, Southwest Africa. Budde-Lund Collection.

SYNTYPES: one male; one female. Reg. no. 1956:10:10:199–200. Landana, Angola, Southwest Africa. Presented by University College, Dundee.

quietum Budde-Lund (1899 : 7)

HOLOTYPE (?): male. Reg. no. 1921:10:18:639. Antoto, Shoa district, Ethiopia. March 1885. (Locality in publication: Let-Marefia.) Collected by V. Ragazzi. Budde-Lund Collection.

stipulatum Budde-Lund (1899 : 5)

SYNTYPES: four males; two females. Reg. no. 1921:10:18:640–645. Cameroons, West Africa. November 1891. Collected by Y. Sjostedt. Budde-Lund Collection.

GELSANA Budde-Lund

abnormis Budde-Lund (1910 : 6)

SYNTYPES: one male; two specimens in very poor condition. Reg. no. 1921:10:18:790–792. Kilimanjaro, Tanganyika. Collected by Y. Sjostedt. Budde-Lund Collection.

GERUTHA Budde-Lund

laevis Budde-Lund (1912c : 6)

SYNTYPES: one male; one female. Reg. no. 1921:10:18:717–718. Escarpment, East Africa. 'Under logs in the forest at Escarpment station. 11.1.1911.' Collected by E. Lonnberg. Budde-Lund Collection.

marginepilosa Budde-Lund (1912c : 6)
SYNTYPES : one male ; four females. Reg. no. 1921:10:18:719–723. Kaffa, Ethiopia. Collected by E. Lonnberg. Budde-Lund Collection.

pila (Budde-Lund) (1898 : 4) [*Eubelum pilum*]
SYNTYPES : one male ; two females. Reg. no. 1921:10:18:724–725. Ru-Nsororo. 2600 m. 9.6.1891. Collected by Stuhlmann. Budde-Lund Collection.

pilosa Budde-Lund (1912c : 6)
SYNTYPE : female. Reg. no. 1921:10:18:726. Shoa district, Ethiopia. Collected by E. Lonnberg. Budde-Lund Collection.

HAPLARMADILLO Dollfus

monocellatus Dollfus (1896c : 400)
HOLOTYPE : female. Reg. no. 1896:1:11:25. Richmond Valley, St Vincent, West Indies. 'Under rotting leaves. 1100 ft. 18th January.' Collected by H. H. Smith. Presented by the West India Committee.

HIALLUM Budde-Lund

hilgendorfi (Budde-Lund) (1898 : 4) [*Eubelum hilgendorfi*]
SYNTYPES : one male ; one female. Reg. no. 1921:10:18:769–770. Runsororo, East Africa. 'Bamboo forest, 9–13.6.1891.' Collected by Stuhlmann and E. Pasha. Budde-Lund Collection.

IGNAMBA Budde-Lund

brevis Budde-Lund (1910 : 5)
SYNTYPES : four females. Reg. no. 1921:10:18:778–781. Kilimanjaro, Tanganyika. Collected by Y. Sjostedt. Budde-Lund Collection.

microps Budde-Lund (1910 : 6)
SYNTYPES : seven females. Reg. no. 1921:10:18:782–789. Kiboscho, Kilimanjaro, Tanganyika. 'In clefts of mountains. 3000 m. February 1906.' Collected by Y. Sjostedt. Budde-Lund Collection.

MESARMADILLO Dollfus

albicornis Budde-Lund (1899 : 13)
SYNTYPES : one male ; one female. Reg. no. 1921:10:18:727–728. N'dian, Cameroons, West Africa. June 1891. Collected by Y. Sjostedt. Budde-Lund Collection.

quadrimaculatus Budde-Lund (1899 : 14)
SYNTYPES : two males. Reg. no. 1921:10:18:733. Cameroons, West Africa. Collected by Y. Sjostedt. Budde-Lund Collection.

tuberculatus Dollfus (1892a : 387)
SYNTYPE : female. Reg. no. 1921:10:18:735. Assinie, West Africa. 1886. Collected by C. Alluaud. Budde-Lund Collection.

MICROCERCUS Budde-Lund

abyssinicus Barnard (1940 : 365)
SYNTYPES : one male ; one female. Reg. no. 1949:2:2:231–232. Djem Djem Forest, Ethiopia. 21.9.1926 and 11.10.1926. Collected and presented by J. Omer-Cooper.

leucocephalus (Budde-Lund) (1895 : 607) [*Periscyphis leucocephalus*]
SYNTYPE : female. Reg. no. 1921:10:18:1267. Rangoon, Burma. July 1887. Collected by L. Fea. Budde-Lund Collection.

PARAPERISCYPHIS Stebbing

stebbingi Collinge (1914b : 207)

HOLOTYPE : male. Reg. no. 1919:4:26:455. Anamali Hills, Madras, S. India. 4000 ft. 22.1.1912. Collected by T. B. Fletcher. Collinge Collection.

PERISCYPHIS Gerstaecker

besi Barnard (1941 : 63)

SYNTYPES : four males ; eight females. Reg. no. 1949:2:2:73–84 (part). Jebel Harir, Western Aden Protectorate. 5000–6000 ft. 10.11.1937. Collected by H. Scott and E. B. Britton. British Museum Expedition to S.W. Arabia, 1937–38.

SYNTYPES : three females. Reg. no. 1949:2:2:73–84 (part). Yemen, 2 miles West of San'a. 8000 ft. 14.2.1938. Collected by H. Scott and E. B. Britton. British Museum Expedition to S.W. Arabia, 1937–38.

SYNTYPE : female. Reg. no. 1949:2:2:73–84 (part). Jebel Jihaf, Western Aden Protectorate. 'Under stones and in damp soil at roots of plants, on steep face of mountain facing north-west. 7700 ft. 4.10.1937.' Collected by H. Scott and E. B. Britton. British Museum Expedition to South West Arabia, 1937–38.

SYNTYPE : female. Reg. no. 1949:2:2:73–84. Wadi Dareija, south-west of Dhala, Western Aden Protectorate. 4600 ft. 9.11.1937. Collected by H. Scott and E. B. Britton. British Museum Expedition to South West Arabia, 1937–38.

bicoloratus Barnard (1941 : 65)

SYNTYPES : three males. Reg. no. 1949:2:2:85–87. Dhala, Western Aden Protectorate. 'From detritus under succulent plants. 4800 ft. 14.9.1937.' Collected by H. Scott. British Museum Expedition to South West Arabia, 1937–38.

cavernicola Omer-Cooper (1926 : 371)

SYNTYPES : one male ; two females. Reg. no. 1921:10:18:1289–1291. Ethiopia. Budde-Lund Collection.

chindeensis Barnard (1932 : 294)

HOLOTYPE : male. Reg. no. 1933:1:25:262. Chinde, mouth of the Zambeze River, Moçambique. 1912. 'In sand dunes near the shore.' Collected by K. H. Barnard. Presented by the South African Museum.

civilis Budde-Lund (1908 : 279)

SYNTYPES : two males ; one female. Reg. no. 1921:10:18:1291–1295. Witu, Kenya. Collected by A. Voeltzkow. Budde-Lund Collection.

hughscotti Barnard (1940 : 362)

SYNTYPES : seventeen males ; twenty-five females. Reg. no. 1949:2:2:201–230. Djem Djem Forest, Ethiopia. c. 8100 ft. 21.9.1926–10.10.1926. Collected and presented by J. Omer-Cooper.

SYNTYPES : twenty-four males ; seventeen females. Reg. no. 1949:2:2:201–230 (part). Addis Ababa, Ethiopia. Over 8000 ft. 10.9.1926. Collected and presented by J. Omer-Cooper.

kunenensis (Barnard) (1924 : 231) [*Periscyphops kunenensis*]

SYNTYPES : seven males ; twelve females. Reg. no. 1933:1:25:263–270. Ovambolande, Kunene River, South West Africa. Collected by K. H. Barnard. Presented by the South African Museum.

latissimus Omer-Cooper (1926 : 395)

HOLOTYPE : male. Reg. no. 1921:10:18:1309. Ethiopia. Budde-Lund Collection.

limbata Omer-Cooper (1926 : 384)

SYNTYPES : two females. Reg. no. 1921:10:18:1310–1311. Kibwesa, Tanganyika. Budde-Lund Collection.

nigricans Omer-Cooper (1926 : 382)

SYNTYPES : three females. Reg. no. 1921:10:18:1312–1314. Locality given in publication : 'Abyssinia, Schoa Galla ; Somaliland'. No locality data with specimen. 9.10.1901. Collected by V. Erlangen. Budde-Lund Collection.

pulcher Budde-Lund (1898 : 7)

HOLOTYPE : female. Reg. no. 1921:10:18:1315. Tanga, East Africa. Collected by Moller. Budde-Lund Collection.

quadrimaculatus Budde-Lund (1908 : 279) [Transferred to *Periscyphis trivialis* Gerst]

SYNTYPES : eleven males ; seven females. Reg. no. 1921:10:18:1316–1327. Manda I., Kenya. 21.2.1903. Collected by A. Voeltzkow. Budde-Lund Collection.

ruficauda Budde-Lund (1908 : 278)

SYNTYPES : fourteen males ; thirteen females ; one other specimen in fragments. Reg. no. 1921:10:18:1328–1339. Manda I., Kenya. 21.2.1903. Collected by A. Voeltzkow. Budde-Lund Collection.

SYNTYPE : female. Reg. no. 1952:4:18:59. Manda I., Kenya. Collected by A. Voeltzkow. Jackson Collection.

subtransversus Omer-Cooper (1926 : 392)

SYNTYPES : one male ; two females. Reg. no. 1921:10:18:1340–1342. Egypt. Budde-Lund Collection.

tamei Omer-Cooper (1923 : 394)

SYNTYPE : one specimen in fragments. Reg. no. 1922:5:18:13–14 (part). Al Amarah, Iraq. 1918. Collected by R. G. Tame. Presented by J. Omer-Cooper.

SYNTYPE : one female. Reg. no. 1922:5:18:13–14 (part). Ruz ('Robat' on label), N.E. of Baghdad. 1918. Collected by W. E. Evans. Presented by J. Omer-Cooper.

SYNTYPES : micropreparations of appendages : six males ; fourteen females. Reg. no. 1922:5:18:15–34. Amara, Iraq. 1918. Collected by R. G. Tame. Presented by J. Omer-Cooper.

trivialis Gerstaecker (1873 : 526)

SYNTYPES : three females. Reg. no. 1921:10:18:1343–1345. Lake Jipe, Kenya. Budde-Lund Collection.

undulata Omer-Cooper (1926 : 373)

SYNTYPES : three males ; five females. Reg. no. 1921:10:18:1346–1353. Bala, Shoa district, Ethiopia. Budde-Lund Collection.

vittatus Omer-Cooper (1926 : 366)

HOLOTYPE : male. Reg. no. 1921:10:18:1354–1359 (part). Obock, Somaliland. Budde-Lund Collection.

PARATYPES : six females. Reg. no. 1921:10:18:1354–1359 (part). Obock, Somaliland. Budde-Lund Collection.

PERISCYPHOPS Hilgendorf

bizonatus Budde-Lund (1899 : 18)

SYNTYPES : three males ; four females. Reg. no. 1921:10:18:736–744. Cameroons, West Africa. 1891. Collected by Y. Sjostedt. Budde-Lund Collection.

silvanus Budde-Lund (1899 : 16)

SYNTYPES : four males ; two females. Reg. no. 1921:10:18:749–753. Cameroons, West Africa. 1891. Collected by Y. Sjostedt. Budde-Lund Collection.

squamatus Budde-Lund (1899 : 20)

SYNTYPE : small fragment only. Reg. no. 1921:10:18:755. Bibundi, Cameroons, Nigeria. August 1891. Collected by Y. Sjostedt. Budde-Lund Collection.

squamosus Budde-Lund (1899 : 21)

SYNTYPE : fragments only. Reg. no. 1921:10:18:756. Bibundi, Cameroons, Nigeria. August 1891. Collected by Y. Sjostedt. Budde-Lund Collection.

triarticulatus (Hilgendorf) (1893 : 152) [*Periscyphis* (*Periscyphops*) *triarticulatus*]

SYNTYPES : one male ; three females. Reg. no. 1921:10:18:760–763. Bismarkburg, Togo, West Africa. March 1891. Collected by Buttner. Budde-Lund Collection.

ROTUNGUS Collinge

pictus Collinge (1916 : 544)

PARATYPE : female. Reg. no. 1919:4:26:541. Kobo, Abor country, Assam, India, 400 ft, 'under bark'. Collected by S. W. Kemp. Presented by W. E. Collinge.

Family SPHAERONISCIDAE

CIRCONISCUS Pearse

spinosus (Collinge) (1918 : 62) [*Paracubaris spinosus*]

SYNTYPES : two males. Reg. no. 1919:4:26:542–543. Mazakuvi River, Guiana. May 1916. 'In decaying wood.' Collected by G. E. Bodkin. Collinge Collection.

SCLEROPACTES Budde-Lund

concinnus Budde-Lund (1885 : 240)

SYNTYPES : two males ; one female ; one other specimen in fragments. Reg. no. 1921:10:18:961–964. Tambillo, Peru. Collected by J. Stolzmann. Budde-Lund Collection.

incicus Budde-Lund (1885 : 241)

HOLOTYPE : male. Reg. no. 1921:10:18:968. Peru. Collected by J. Stolzmann. Budde-Lund Collection.

SPHAEROBATHYTROPA Verhoeff

ribauti Verhoeff (1908b : 171)

SYNTYPES : two females. Reg. no. 1908:6:1:15–16. St Beat, Pyrenees, France. Collected by Ribaut. Purchased from K. W. Verhoeff.

SPHAERONISCUS Budde-Lund

frontalis Richardson (1914 : 31)

SYNTYPE : male. Reg. no. 1928:5:1:84–87 (part). Buenavista, nr Viota, Colombia. Collected by and purchased from O. Fuhrmann.

SYNTYPES : two males ; two females. Reg. no. 1928:5:1:84–87 (part). Argelia, nr Viota, Colombia. Collected by and purchased from O. Fuhrmann.

Family ACTOECIIDAE

ACTOECIA Dana

opihensis Chilton (1901 : 132)

SYNTYPES : one male ; two females. Reg. no. 1900:11:61–64. Timaru, New Zealand. Presented by C. Chilton.

SYNTYPES : one male ; one female. Reg. no. 1921:10:18:1072–1073. Timaru, New Zealand. Budde-Lund Collection.

Family ARMADILLIDAE

ACANTHONISCUS Kinahan

spiniger Kinahan (1859 : 197)

HOLOTYPE : female. Reg. no. 1973:478:1 (original registration no. 1845:118). Jamaica, West Indies. Purchased from Mr Gosse.

AKERMANIA Collinge

spinosa Collinge (1919 : 230)

SYNTYPES : four males ; four females ; four other specimens with genitalia missing. Reg. no. 1919:4:26:282–291. Umhlali, Winkle Spruit, South Africa. May 1916. Collected by C. Akerman. Collinge Collection.

SYNTYPES : four females. Reg. no. 1933:1:25:413–417. Umhlali, Winkle Spruit, South Africa. Collected by C. Akerman. Presented by the South African Museum.

ANCHICUBARIS Collinge

fongosiensis Collinge (1920 : 484)

SYNTYPES : twelve males ; twenty females. Reg. no. 1919:4:26:504–518. Mt Fongosi, Zululand, Natal. July 1917. Collected by W. E. Jones. Collinge Collection.

SYNTYPES : forty-three males ; forty-one females. Reg. no. 1933:1:25:851–870. Mt Fongosi, Zululand, Natal. July 1917. Collected by W. E. Jones. Presented by the South African Museum.

ARMADILLO Dumeril

affinis (Miers) (1877b : 666) [*Cubaris affinis*]

SYNTYPES : one male ; four females. Reg. no. 1879:21:6. Cayenne, Guiana. Presented by A. Wrzésniowsky.

albomarginatus Dollfus (1892c : 3)

SYNTYPE : male. Reg. no. 1911:11:8:9755. Route de Ouady-Hafaf at Aîn-Djeddy, Dead Sea. Collected by T. Barrois. Norman Collection.

SYNTYPE : female. Reg. no. 1921:10:18:2434. Karytein, Syria. Collected by T. Barrois. Budde-Lund Collection.

albospinosus Dollfus (1900 : 522)

SYNTYPE : female. Reg. no. 1904:11:5:8–9 (part). Makaweli, Kauai I., Hawaiian Is., 3000 ft. 1897. Presented by the Joint Committee for investigating the Fauna of the Sandwich Islands.

SYNTYPE : male. Reg. no. 1904:11:5:8–9 (part). Kawaihoa, Oahu I., Hawaiian Is. Collected by Perkins. Presented by the Joint Committee for investigating the Fauna of the Sandwich Islands.

ausseli Dollfus (1893 : 48)

SYNTYPES : three females. Reg. no. 1921:10:18:1095–1096. La Laguna, Tenerife, Canary Is. 'Agua Garcia, laurel forest (probably Las Mercedes Forest), 800 m.' Collected by H. Aussel. Budde-Lund Collection.

SYNTYPE : female. Reg. no. 1908:6:1:44. Tenerife, Canary Is. Purchased from K. W. Verhoeff.

bituberculatus Budde-Lund (1912a : 36)

SYNTYPE : female. Reg. no. 1921:10:18:2450. Torbay, South West Australia. 'Sta. 162.' Budde-Lund Collection.

brevicornis Budde-Lund (1913a : 69)

SYNTYPES : four females. Reg. no. 1921:10:18:2451–2454. New South Wales, Australia. Budde-Lund Collection.

cinctus Budde-Lund (1896 : 41)

SYNTYPES : two females ; one other broken specimen. Reg. no. 1921:10:18:2466–2468. Kasos I., Greece, Mediterranean Sea. Collected by E. von Oertzen. Budde-Lund Collection.

collinus Budde-Lund (1895 : 604)

SYNTYPES : two specimens both in fragments. Reg. no. 1921:10:18:2518–2519. Carim Hills, Ascinii Ghecu, Burma. 1300–1400 m. Collected by L. Fea. Budde-Lund Collection.

conglobator Budde-Lund (1904 : 124)

HOLOTYPE : female. Reg. nos. 1921:10:18:1663 & 1921:10:18:2520 (fragments from holotype). Pulo, Penang, Malaysia. 600–750 m. February 1879. Collected by L. Fea and Loria. Budde-Lund Collection.

egens Budde-Lund (1904 : 124)

HOLOTYPE : broken. Reg. no. 1902:12:4:16. Malawi (formerly Nyasaland), Central Africa. Collected and presented by H. H. Johnston.

erythroleucus Budde-Lund (1904 : 98)

HOLOTYPE (?): female. Reg. no. 1921:10:18:2469. Crimea, Ukraine, USSR. Budde-Lund Collection.

flavus Budde-Lund (1912a : 37)

SYNTYPES : one male ; one female. Reg. no. 1921:10:18:2415–2416. Mundaring Weir, West Australia. 'Sta. 101.' 9.8.1905.

harsadiensis (Barnard) (1940 : 359)

SYNTYPES : one male ; three females ; three other specimens in fragments. Reg. no. 1949:2:2:171–178. Shore of Hora Harsadi, lakes of Addas, Ethiopia. 7000 ft. 2–3.12.1926. Collected and presented by J. Omer-Cooper.

immotus Budde-Lund (1904 : 122)

SYNTYPES : one male ; two females. Reg. no. 1921:10:18:2523–2525. Pulo, Penang I., Malaysia. 600–700 m. March 1870. Collected by L. Fea and Loria. Budde-Lund Collection.

inconspicuus Miers (1876 : 225) [Transferred to *Spherillo danae* Heller]

HOLOTYPE : female. Reg. no. 1973:477:1 (original reg. no. 1845:4). New Zealand. Presented by Col. Bolton.

integer Budde-Lund (1912a : 35)

SYNTYPES : three males. Reg. no. 1921:10:18:2426–2428. Torbay, Western Australia. 'Sta. 162.' 19.8.1905. Budde-Lund Collection.

intermixtus Budde-Lund (1904 : 126)

SYNTYPES : two males ; one other specimen in fragments. Reg. no. 1921:10:18:2526–2527. The Caves, Selangore, Malaysia. 1897. Collected by H. N. Ridley. Budde-Lund Collection.

SYNTYPES : twenty-nine males ; nine females. Reg. no. 1898:4:11:1–10. The Caves, Selangore, Malaysia. 1897. Collected and presented by H. N. Ridley.

lifuensis (Stebbing) (1900 : 653) [*Cubaris lifuensis*]

SYNTYPES : one male ; six females. Reg. no. 1906:4:19:81–88. Lifu I., Loyalty Is., Pacific Ocean. Presented by A. Willey.

SYNTYPES : one male ; two females. Reg. no. 1928:12:1:1553–1555. Lifu I., Loyalty Is. Stebbing Collection.

macmahoni Chilton (1901 : 149)

SYNTYPES : one male ; one female. Reg. no. 1900:11:1:16–17. Kenepuru, Marlborough, New Zealand. Presented by C. Chilton.

mayeti Simon (1885 : 7)

SYNTYPES : one male ; one female. Reg. no. 1921:10:18:2470–2471. Sfax, Tunisia. Collected by V. Mayer. Budde-Lund Collection.

miser Budde-Lund (1904 : 121)

HOLOTYPE : male. Reg. no. 1921:10:18:2528. Victoria, Australia. Collected by Hauschild. Budde-Lund Collection.

montanus Budde-Lund (1904 : 99)

SYNTYPES : one male ; five females. Reg. no 1921:10:18:2472–2477. Djebel Tarchuna, Tripoli, Libya. Collected by G. Rohlfs. Budde-Lund Collection.

nigromarginatus Budde-Lund (1904 : 127)

Holotype : male. Reg. no. 1902:12:4:6. Selangore, Malaysia. 'In caves, 1897.' Collected and presented by H. N. Ridley.

officinalis syriaca Dollfus (1892c : 2)

Syntype : female. Reg. no. 1892:12:6:2. Syria. 1886. Collected by L. Bleuse. Presented by D'Arcy Thomson (ex Dollfus collection).

Syntypes : two females. Reg. no. 1911:11:8:9750–9751. Syria. 1886. Collected by L. Bleuse. Norman Collection.

Syntype : female. Reg. no. 1956:10:10:137. Syria. Collected by L. Bleuse. Presented by University College, Dundee.

oxyzomus (Barnard) (1940 : 360) [*Cubaris oxyzomus*]

Syntypes : two females. Reg. no. 1949:2:2:179–180. Djem Djem Forest, Ethiopia. 8000 ft. 20.9.1926. Collected and presented by J. Omer-Cooper.

piger Budde-Lund (1896 : 42)

Holotype : female. Reg. no. 1921:10:18:2494. Sitía, Crete. Budde-Lund Collection.

pilularis Say (1818 : 432) [Transferred to *Armadillidium vulgare* (Latr.)]

Syntype : female. Reg. no. 1973:510:1. North America. Presented by T. Say.

proximatus Budde-Lund (1904 : 122)

Syntypes : one male ; three females. Reg. no. 1921:10:18:2572–2578. Telang, Borneo. Budde-Lund Collection.

pygmaeus Budde-Lund (1912a : 36)

Syntypes : seven females. Reg. no. 1921:10:18:2495–2501. Guildford, Western Australia. 'Sta. 103'. 19.5.1905. Budde-Lund Collection.

sharpi Dollfus (1900 : 523)

Holotype : female. Reg. no. 1904:11:5:13. Kauai I., Hawaiian Is. 4000 ft. August 1896. Collected by Perkins. Presented by the Joint Committee for Investigating the Fauna of the Sandwich Islands.

tenuipunctatus Dollfus (1896c : 389)

Syntypes : two males ; one female. Reg. no. 1896:1:11:2–3. Mustique I., Windward Is. 'Beaten from bushes. June.' Collected by H. H. Smith. Presented by the West India Committee.

trifolium Dollfus (1890 : 1)

Holotype : female. Reg. no. 1927:5:14:1. San Tiago, Cape Verdi Is. August 1873. 'Challenger' Collection.

viticola Dollfus (1896c : 396)

Syntype : male. Reg. no. 1896:1:11:9–11 (part). Chantilly, Grenada I., Windward Is. 1400 ft. 23 March. 'Hillside, edge of forest, beaten from vines and brush.' Collected by H. H. Smith. Presented by the West India Committee.

Syntypes : one male ; one female. Reg. no. 1896:1:11:9–11 (part). Balthazar, Grenada I., Windward Is. 250 ft. 19 March and 17 August. 'Second-growth woods, beaten from vines and brush.' Collected by H. H. Smith. Presented by the West India Committee.

wilsmorei (Nicholls & Barnes) (1926 : 150) [*Cubaris wilsmorei*]

Syntypes : four males ; eight females ; five other specimens tightly rolled up. Reg. no. 1926:12:1:30–34. Banks of Frankland River, Nornalup, South West Australia. 'Under logs'. Collected and presented by G. E. Nicholls.

zebricolor (Stebbing) (1900:656) [*Cubaris zebricolor*]

Holotype : fragmented. Reg. no. 1906:4:19:93. Lifu I., Loyalty Is. Presented by A. Willey.

BETHALUS Budde-Lund

barbertoni Barnard (1932 : 312)

Syntypes : three males ; four females ; two other specimens in fragments. Reg. no. 1933:1:25:365–371. Barberton, Transvaal, South Africa. Presented by the South African Museum.

Syntypes : one male ; three females. Reg. no. 1933:1:25:372–375. Inhambane, Moçambique. Collected by K. H. Barnard. Presented by the South African Museum.

barnardi (Collinge) (1920 : 482) [*Cubaris barnardi*]

Paratypes: forty specimens (males, females and juveniles). Reg. no. 1933:1:25:398–412. Mt Fongosi, Zululand, South Africa. January 1917. Collected by W. E. Jones. Presented by the South African Museum.

carinatus (Budde-Lund) (1908 : 272) [*Armadillo carinatus*]

Syntypes : nine males ; twenty-three females. Reg. no. 1921:10:18:1189–1200. Tananarive, Madagascar. June 1897. Budde-Lund Collection.

cassida (Budde-Lund) (1908 : 274) [*Armadillo cassida*]

Holotype : few fragments only. Reg. no. 1921:10:18:1201. Sahana, Madagascar. September 1904. Budde-Lund Collection.

depressus (Dollfus) (1896c : 390) [*Armadillo depressus*]

Holotype : female. Reg. no. 1896:1:11:1. Chateaubelais, St Vincent I., West Indies. August 1889–91. Collected by H. H. Smith. Presented by the West India Committee.

emarginatus Budde-Lund (1910 : 12)

Syntypes : three males ; three females. Reg. no. 1921:10:18:1204–1208. Mkulimusi, nr Tanga, Tanganyika. June 1906. Budde-Lund Collection.

emunitus (Budde-Lund) (1904 : 129) [*Armadillo emunitus*]

Syntypes : one male ; two females. Reg. no. 1921:10:18:2521–2522. Thailand. Budde-Lund Collection.

griseoalbus (Dollfus) (1895 : 347) [*Armadillo griseoalbus*] [Transferred to *Bethalus limbatus* (Brandt)]

Syntypes : two males. Reg. no. 1921:10:18:1218. Matjesfontein, South Africa. Collected by E. Simon. Budde-Lund Collection.

latifrons (Budde-Lund) (1904 : 132) [*Armadillo latifrons*] [Transferred to *Bethalus mucidus* (Budde-Lund)]

Syntypes : one male ; two females. Reg. no. 1921:10:18:1219–1221. Natal, South Africa. 1840–45. Collected by A. Wahlberg. Budde-Lund Collection.

macrodens Barnard (1932 : 311)

Syntypes : two males ; one female. Reg. no. 1933:1:25:361–364. Groot Vaders Bosch, Langeberg Mts, nr Heidelberg, Cape Province, South Africa. Collected by K. H. Barnard. Presented by the South African Museum.

panurus (Budde-Lund) (1904 : 131) [*Armadillo panurus*]

Holotype : male. Reg. no. 1921:10:18:1132. Natal, South Africa. Collected by A. Wahlberg. Budde-Lund Collection.

pretoriensis (Dollfus) (1895 : 348) [*Armadillo pretoriensis*]

Syntypes : one male ; one female (fragments only). Reg. no. 1921:10:18:1227. Pretoria, South Africa. Collected by E. Simon. Budde-Lund Collection.

rhodesiae Barnard (1932 : 305)

Syntypes : one male ; two females. Reg. no. 1933:1:25:328–330. Bulawayo, South Rhodesia. Collected by R. W. E. Tucker. Presented by the South African Museum.

stricticauda (Dollfus) (1895 : 348) [*Armadillo stricticauda*]

Syntypes : one male ; one female. Reg. no. 1921:10:18:1229. Grotte de Makapan, Transvaal, South Africa. Collected by E. Simon. Budde-Lund Collection.

tradouwi Barnard (1932 : 310)

Syntypes : two males ; six females. Reg. no. 1933:1:25:353–360. Tradouw Pass, Langeberg Mts, Cape Province, South Africa. Collected by K. H. Barnard. Presented by the South African Museum.

BUDDELUNDIA Michaelson

albomaculatus Budde-Lund (1912a : 33)

Syntypes : one male ; one female. Reg. no. 1921:10:18:2432–2433. Broome Hill, West Australia. 'Sta. 158'. 24.8.1905. Budde-Lund Collection.

binotatus Budde-Lund (1912a : 24)
SYNTYPES : two females. Reg. no. 1921:10:18:1435–2436. Boorabbin, West Australia. 'Sta. 95'. 3.7.1905. Budde-Lund Collection.

bipartitus Budde-Lund (1912a : 24)
SYNTYPES : two males ; eleven females. Reg. no. 1921:10:18:2437 (fragments) ; 2438–2449. South West Australia. Budde-Lund Collection.

callosus Budde-Lund (1912a : 28)
SYNTYPES : four males ; three females. Reg. no. 1921:10:18:2455–2461. Northampton, West Australia. 'Sta. 71'. 15.8.1905. Budde-Lund Collection.

cinerascens Budde-Lund (1912a : 26)
SYNTYPES : one male ; two females. Reg. no. 1921:10:18:2464–2465. Rottnest I., West Australia. 'Sta. 121'. 6–13.10.1905. Budde-Lund Collection.

frontosus Budde-Lund (1912a : 30)
HOLOTYPE : male (few small fragments). Reg. no. 1921:10:18:2417. Coolgardie, West Australia. 'Sta. 94'. 3.7.1905. Budde-Lund Collection.

inaequalis Budde-Lund (1912a : 27)
SYNTYPES : one male ; two females. Reg. no. 1921:10:18:2418–2420. Fremantle, West Australia. 20.5.1905. Budde-Lund Collection.

labiatus Budde-Lund (1912a : 20)
HOLOTYPE : male. Reg. no. 1907:5:6:14. Lake Miranda, West Australia. Collected and presented by G. H. Ince.
FRAGMENT OF HOLOTYPE : Reg. no. 1921:10:18:2425. Budde-Lund Collection.

laevigatus Budde-Lund (1912a : 23)
SYNTYPES : two females. Reg. no. 1921:10:18:2430–2431. Day Dawn, West Australia. 'Sta. 76'. 9.7.1905. Budde-Lund Collection.

lateralis Budde-Lund (1913a : 67)
HOLOTYPE : male. Reg. no. 1921:10:18:2429. New South Wales, Australia. Budde-Lund Collection.

monticola Budde-Lund (1912a : 21)
HOLOTYPE : female (fragments). Reg. no. 1921:10:18:2478. Mt Robinson, Kalgoorlie, West Australia. 1.7.1905. Budde-Lund Collection.

nigripes Budde-Lund (1912a : 33)
SYNTYPES : nine females. Reg. no. 1921:10:18:2479–2487. Bunbury, West Australia. 'Sta. 142'. 25.7.1905. Budde-Lund Collection.

opacus Budde-Lund (1912a : 29)
SYNTYPES : three females. Reg. no. 1921:10:18:2491–2493. Gooseberry Hill, West Australia. 'Sta. 152'. 31.5.1905. Budde-Lund Collection.

quadritracheata Budde-Lund (1913a : 68)
SYNTYPES : one male ; one female. Reg. no. 1921:10:18:2502–2503. Condobolin, New South Wales, Australia. 17.10.1900. Budde-Lund Collection.

rugifrons Budde-Lund (1912a : 28)
SYNTYPES : three females. Reg. no. 1921:10:18:2504–2505. South West Australia. Budde-Lund Collection.

sulcatus Budde-Lund (1912a : 22)
SYNTYPES : one male ; two females. Reg. no. 1921:10:18:2508–2510. Eradu, West Australia. 'Sta. 80'. 13.7.1905. Budde-Lund Collection.

tomentosus Budde-Lund (1912a : 34)
SYNTYPE : specimen in fragments. Reg. no. 1921:10:18:2511. Baba Head, Edel Land, West Australia. 7.9.1905. Budde-Lund Collection.

DIPLOEXOCHUS Brandt

aenigma Barnard (1932 : 372)
SYNTYPE : female. Reg. no. 1933:1:25:801–802. Stella Bush, Durban, Natal, South Africa. Collected by K. H. Barnard. Presented by the South African Museum.

aerarius Barnard (1937 : 162)

Syntypes: three females. Reg. no. 1937:11:10:168–169. Steinkopf, Namaqualand, Cape Province. March 1935. Collected by R. F. Lawrence and A. J. Hesse. Presented by the South African Museum.

alberti Barnard (1932 : 352)

Syntypes: six males; seven females. Reg. no. 1933:1:25:606–616. Zwartberg Pass, Prince Albert Division, Cape Province. 5500 ft. 1929. Collected by K. H. Barnard. Presented by the South African Museum.

albescens Budde-Lund (1909b : 56)

Syntypes: five males; three females. Reg. no. 1921:10:18:1097–1105. Port Nolloth, Klein-Namaland, South West Africa. April 1905. Collected by L. Schultze. Budde-Lund Collection.

alticola Barnard (1932 : 348)

Syntypes: one female; two other specimens in fragments. Reg. no. 1933:1:25:581–582. Zwartberg Pass, Prince Albert Division, Cape Province, South Africa. Collected by K. H. Barnard. Presented by the South African Museum.

bituberculatus Budde-Lund (1910 : 11)

Holotype: in fragments. Reg. no. 1921:10:18:1094. Kibonoto, Tanganyika. 1300–1800 m. 'In leaf mould.' November 1905. Collected by Y. Sjostedt. Budde-Lund Collection.

canariensis (Dollfus) (1893 : 48) [*Armadillo canariensis*]

Syntypes: one male; one female. Reg. no. 1911:11:8:9753–9754. Canary Is. Collected by C. Alluaud. Norman Collection.

Syntype: one female and one other specimen, both in fragments. Reg. no. 1921:10:18:1093. Fuerteventura I., Canary Is. Collected by C. Alluaud. Budde-Lund Collection.

castor Barnard (1932 : 24)

Syntypes: nine males; seventeen females. Reg. no. 1933:1:25:738–754. Kamiesberg, Cape Province, South Africa. 1931. Collected by K. H. Barnard. Presented by the South African Museum.

celsicauda Barnard (1932 : 366)

Syntypes: twenty-eight males; fifty-one females. Reg. no. 1933:1:25:755–774. Vanrhynsdorp, Cape Province, South Africa. 1931. Collected by K. H. Barnard. Presented by the South African Museum.

cingulatus Barnard (1932 : 373)

Syntypes: one female; one other specimen in fragments. Reg. no. 1933:1:25:804–805. Stella Bush, Durban, Natal, South Africa. 1912. Collected by K. H. Barnard. Presented by the South African Museum.

coloratus Barnard (1932 : 342)

Syntypes: seven males; eleven females. Reg. no. 1933:1:25:533–540. Kridouw, between Citrusdal and Clanwilliam, Cape Province, South Africa. 1931. Collected by K. H. Barnard. Presented by the South African Museum.

congener (Budde-Lund) (1904 : 108) [*Armadillo congener*]

Syntypes: one male; one female; one other specimen in fragments. Reg. no. 1921:10:18:1089–1090. Rio Nabilecche, 'in the interior of Brazil'. July 1897. Collected by G. Boggiani. Budde-Lund Collection.

conisaleus Barnard (1932 : 359)

Syntypes: seven females. Reg. no. 1933:1:25:650–656. Inchanga, Natal, South Africa. 1917. Collected by K. H. Barnard. Presented by the South African Museum.

crassus (Budde-Lund) (1904 : 105) [*Armadillo crassus*]

Syntype: male. Reg. no. 1921:10:18:1087. Sao Tomé, Gulf of Guinea. Collected by R. Greef. Budde-Lund Collection.

disjunctus Barnard (1932 : 364)

Syntypes: one male; nine females; one other specimen in fragments. Reg. no. 1933:1:25:730–737. Riversdale, Langeberg Range, Cape Province, South Africa, 1926–27. Collected by K. H. Barnard. Presented by the South African Museum.

dugesi (Dollfus) (1896a : 46) [*Armadillo dugesi*]

SYNTYPE : female. Reg. no. 1921:10:18:1104. Corritos, Silao, Mexico. Collected by Dugès. Budde-Lund Collection.

ecaudatus Barnard (1932 : 356)

SYNTYPES : forty-seven males, females and juveniles. Reg. no. 1933:1:25:626–633. Zwartberg, Caledon, Cape Province, South Africa. 1918. Collected by K. H. Barnard. Presented by the South African Museum.

festivus (Budde-Lund) (1904 : 112) [*Armadillo festivus*]

SYNTYPES : two females and one other specimen, all in fragments. Reg. no. 1921:10:18:1106–1107. Port Elizabeth, South Africa. 15.12.1898. Collected by Brauns. Budde-Lund Collection.

furcatus Barnard (1932 : 364)

SYNTYPES : six males ; twenty-one females. Reg. no. 1933:1:25:720–729. River Zonder End Mounts, Cape Province, South Africa. Collected by K. H. Barnard. Presented by the South African Museum.

galapagoensis (Miers) (1877a : 74) [*Cubaris galapagoensis*]

HOLOTYPE : female. Reg. no. 1876:18:3. Santa Maria I. (formerly Charles I.), Galapagos Is., Pacific Ocean. Collected and presented by W. E. Cookson.

gigas (Miers) (1877b : 666) [*Cubaris gigas*]

SYNTYPES : two males ; one female. Reg. no. 1941:6:27:10–13. San Juan, Nicaragua, Central America. Collected by and purchased from Sallé.

glomus (Budde-Lund) (1898 : 8) [*Armadillo glomus*]

SYNTYPES : three males ; seven females. Reg. no. 1921:10:18:1113–1121. Zanzibar, East Africa. Collected by A. Voeltzkow. Budde-Lund Collection.

SYNTYPE : male. Reg. no. 1956:10:10:139. Zanzibar I., East Africa. Collected by A. Voeltzkow. Presented by University College, Dundee.

gordoniensis Barnard (1932 : 370)

SYNTYPES : twenty-four males ; forty-six females. Reg. no. 1933:1:25:781–800. Kakamas, Cape Province, South Africa. Collected by K. H. Barnard. Presented by the South African Museum.

hypselos Barnard (1932 : 357)

SYNTYPES : thirty males, females and juveniles. Reg. no. 1933:1:25:634–643. Krantzkop, Natal, South Africa. 1917. Collected by K. H. Barnard. Presented by the South African Museum.

hypsinephes Barnard (1932 : 362)

SYNTYPES : three males ; nine females. Reg. no. 1933:1:25:675–684. Zwartberg Pass, Prince Albert Division, Cape Province, South Africa. 4000–5000 ft. 1929. Collected by K. H. Barnard. Presented by the South African Museum.

kaokoensis Barnard (1932 : 333)

SYNTYPES : two males ; one female. Reg. no. 1933:1:25:454–456. Kaoko Otavi, Kaokoveld, South West Africa. Collected by K. H. Barnard. Presented by the South African Museum.

kogmani Barnard (1931 : 340)

SYNTYPES : two males ; sixteen females. Reg. no. 1933:1:25:503–514. Kogman's Kloof, between Ashton and Montagu, Cape Province, South Africa. Collected by K. H. Barnard. Presented by the South African Museum.

limenites Barnard (1932 : 361)

SYNTYPES : twenty-two males ; eighteen females ; two juveniles. Reg. no. 1933:1:25:659–674. Mossel Bay, Cape Province, South Africa. Collected by W. F. Purcell. Presented by the South African Museum.

longipes (Budde-Lund) (1909b : 55) [*Armadillo longipes*]

SYNTYPE : female. Reg. no. 1921:10:18:1123. Okahandja, South West Africa. Collected by L. Schultze. Budde-Lund Collection.

makuae Barnard (1932 : 360)

SYNTYPE : specimen in fragments. Reg. no. 1933:1:25:657–658. Masiene, Portuguese East Africa. Collected by R. F. Lawrence. Presented by the South African Museum.

meiringi Barnard (1932 : 351)

SYNTYPES : two females. Reg. no. 1933:1:25:604–605. Meirings Poort Berg, Zwartberg Range, South Africa. 6900 ft. 1932. Collected by K. H. Barnard. Presented by the South African Museum.

montagui Barnard (1932 : 571)

SYNTYPES : two males ; one female. Reg. no. 1933:1:25:571–574. Montagu, Cape Province, South Africa. 1922. Collected by K. H. Barnard. Presented by the South African Museum.

nanus Budde-Lund (1910 : 12)

HOLOTYPE : few fragments only. Reg. no. 1921:10:18:1125. Acacia forest, at Ngare na Nyuki, Mt Meru, Tanganyika. Budde-Lund Collection.

nebulosus Barnard (1932 : 363)

SYNTYPES : five males ; twenty-eight females. Reg. no. 1933:1:25:705–719. Swellendam Mts, Langeberg Range, Cape Province, South Africa. 1925. Collected by K. H. Barnard. Presented by the South African Museum.

obliquidens Barnard (1932 : 330)

SYNTYPES : two males ; two females ; two other specimens in fragments. Reg. no. 1933:1:25:430–435. Messina, Transvaal, South Africa. Collected by R. W. E. Tucker. Presented by the South African Museum.

orphanus Barnard (1932 : 347)

SYNTYPES : five females ; two other specimens in fragments. Reg. no. 1933:1:25:575–580. Weeskind (Orphan) Kop, west edge of the Kamiesberg overlooking Garies, Cape Province, South Africa. Collected by K. H. Barnard. Presented by the South African Museum.

ovampoensis (Barnard) (1924 : 232) [*Cubaris ovampoensis*]

SYNTYPES : two males ; three females ; three other specimens tightly rolled up. Reg. no. 1933:1:25:425–429. Namakunde, Ovamboland, South Africa. Collected by K. H. Barnard. Presented by the South African Museum.

pachytos Barnard (1932 : 337)

SYNTYPES : four males ; twenty-five females ; four other specimens tightly rolled up. Reg. no. 1933:1:25:816–830. Wellington Mts, Cape Province, South Africa. Collected by K. H. Barnard. Presented by the South African Museum.

pauperculus Barnard (1932 : 350)

SYNTYPES : two males ; five females ; two other specimens in fragments. Reg. no. 1933:1:25:591–600. Fore Bay, nr Mossel Bay, Cape Province, South Africa. Collected by K. H. Barnard. Presented by the South African Museum.

pisum (Budde-Lund) (1886 : 32) [*Armadillo pisum*]

SYNTYPES : two males ; two females ; one other specimen in fragments. Reg. no. 1921:10:18:1133–1135. Key West, Florida, North America. Collected by E. Lonnberg. Budde-Lund Collection.

pollex Barnard (1936 : 10)

SYNTYPE : female. Reg. no. 1936:7:13:50. Le Pouce, Mauritius. 2400 ft. Collected and presented by R. F. Lawrence.

polythele Barnard (1932 : 350)

SYNTYPES : one male ; one female. Reg. no. 1933:1:25:601–603. Zwartberg Pass, Prince Albert Division, Cape Province, South Africa. 1929. Collected by K. H. Barnard. Presented by the South African Museum.

quadrimaculatus Budde-Lund (1909b : 54)

SYNTYPES : two males ; one female in fragments. Reg. no. 1921:10:18:1138–1140. Keetmanshoop, Gross-Namaland, South West Africa. Collected by L. Schultze. Budde-Lund Collection.

rhodesiensis Barnard (1932 : 349)

SYNTYPES : one male ; three females ; one specimen in fragments. Reg. no. 1933:1:25:583–590. Bulawayo, South Rhodesia. 'In nests of *Pheidole* ants.' Collected by W. R. E. Tucker. Presented by the South African Museum.

rufescens Budde-Lund (1909b : 56)

SYNTYPES : seven males ; six females. Reg. no. 1921:10:18:1141–1152. Klein-Namaland, Kamagas, South Africa. June 1904. Collected by L. Schultze. Budde-Lund Collection.

saldanhae Barnard (1932 : 334)

SYNTYPES : three males ; three females. Reg. no. 1933:1:25:457–461. Saldanha Bay, Cape Province, South Africa. 1912. Collected by K. H. Barnard. Presented by the South African Museum.

salisburyensis Barnard (1932 : 327)

SYNTYPES : one male ; three females ; one other specimen in fragments. Reg. no. 1933:1:25:420–424. Salisbury, Rhodesia. Collected by R. W. E. Tucker. Presented by the South African Museum.

silvarum (Dollfus) (1896c : 393) [*Armadillo silvarum*]

SYNTYPES : one male ; three females. Reg. no. 1896:1:11:4–7 (part). West Indies. Collected by H. H. Smith. Presented by the West India Committee.

SYNTYPE : male. Reg. no. 1896:1:11:4–7 (part). Cumberland Valley, Leeward Is. 1000 ft. 2 December. 'Open, damp ground, under a stone.' Collected by H. H. Smith. Presented by the West India Committee.

SYNTYPES : two males ; five females. Reg. no. 1896:1:11:4–7 (part). St Vincent, Windward Is. 'Pretty common under rubbish, forest below 2000 ft.' Collected by H. H. Smith. Presented by the West India Committee.

SYNTYPE : male. Reg. no. 1896:1:11:4–7 (part). Leeward Is. 'Forest, dry hillside, near Chateaubelair. 1000 ft. October 11th. Under stone.' Collected by H. H. Smith. Presented by the West India Committee.

SYNTYPE : female. Reg. no. 1921:10:18:1153. St Vincent, Windward Is. Collected by H. H. Smith. Budde-Lund Collection.

steenbrasi Barnard (1932 : 335)

SYNTYPE : female. Reg. no. 1933:1:25:462–465. Mouth of Steenbras River, South of Gordon's Bay, Cape Province, South Africa. Collected by W. F. Purcell. Presented by the South African Museum.

tabularis Barnard (1932 : 354)

SYNTYPES : fifty males, females and juveniles. Reg. no. 1933:1:25:616–625. Table Mt, Cape Province, South Africa. Collected by K. H. Barnard. Presented by the South African Museum.

tugelae Barnard (1932 : 353)

SYNTYPES : two females ; one other specimen in fragments. Reg. no. 1933:1:25:612–615. Krantzkop, nr south bank of Tugela River, Natal, South Africa. 'In ants' nest under stones.' Collected by K. H. Barnard. Presented by the South African Museum.

verrucosus (Budde-Lund) (1904 : 104) [*Armadillo verrucosus*]

SYNTYPES : two males ; two females. Reg. no. 1921:10:18:1177–1180. Guayaquil, Ecuador. 'Under bark of trees 10.7.1903.' Collected by F. Buchwald. Budde-Lund Collection.

zigzag (Dollfus) (1896c : 397) [*Armadillo zigzag*]

HOLOTYPE : male. Reg. no. 1896:1:11:18. St Vincent, Windward Is. 'Forest, damp ground under rubbish. 1000 ft.' Collected by H. H. Smith. Presented by the West India Committee.

zwartbergensis Barnard (1932 : 363)

SYNTYPES : fifteen males ; thirty-eight females. Reg. no. 1933:1:25:685–704. Seweweekspoort Berg, Zwartberg Range, nr Ladysmith, Cape Province, South Africa. 1928. Collected by K. H. Barnard. Presented by the South African Museum.

GLOMERULUS Budde-Lund

microps (Budde-Lund) (1904 : 116) [*Armadillo microps*]

SYNTYPES : two males ; one female. Reg. no. 1921:10:18:1181–1183. Peak Downs, Queensland, Australia. Budde-Lund Collection.

MERULANA Budde-Lund

bicarinata (Budde-Lund) (1913a : 65) [*Sperillo* (*Merulana*) *bicarinata*]

SYNTYPE : female. Reg. no. 1921:10:18:807. New South Wales, Australia. Collected by Michaelsen. Budde-Lund Collection.

canaliculata (Budde-Lund) (1904 : 74) [*Spherillo canaliculatus*]

SYNTYPES : one male ; one female. Reg. no. 1921:10:18:827–828. Chatham I., Pacific Ocean. Collected by Schauinsland. Budde-Lund Collection.

iniqua (Budde-Lund) (1904 : 74) [*Spherillo iniquus*]

SYNTYPES : one male ; two females. Reg. no. 1921:10:18:864–866. Cape York, Queensland, Australia. Collected by Dämel. Budde-Lund Collection.

translucida (Budde-Lund) (1885 : 290) [*Armadillo translucidus*]

HOLOTYPE : female (with two juveniles). Reg. no. 1921:10:18:928. Nouméa, New Caledonia, Pacific Ocean. Collected by Savés. Budde-Lund Collection.

translucida gracilior Verhoeff (1926b : 306)

HOLOTYPE : female. Reg. no. 1928:7:4:16. Hienghène, New Caledonia. Purchased from K. W. Verhoeff.

NESODILLO Verhoeff

bocki Verhoeff (1938a : 9)

SYNTYPES : two females. Reg. no. 1938:7:7:56–57. Gilbert's I., Pacific Ocean. Collected on Prof. S. Bock's Pacific Expedition, 1917–18. Purchased from K. W. Verhoeff.

sarasini Verhoeff (1926b : 280)

SYNTYPE : male. Reg. no. 1928:7:4:17. New Caledonia. Purchased from K. W. Verhoeff.

SYNTYPE : female. Reg. no. 1938:7:7:58. New Caledonia. Purchased from K. W. Verhoeff.

schellenbergi Verhoeff (1928a : 211)

SYNTYPE : female. Reg. no. 1928:7:4:8. Formosa. Purchased from K. W. Verhoeff.

ORODILLO Verhoeff

sauteri Verhoeff (1928a : 206)

SYNTYPES : one male ; one female. Reg. no. 1928:7:4:1–2. Pilam, Taiwan. Purchased from K. W. Verhoeff.

PERICEPHALUS Budde-Lund

feae (Budde-Lund) (1895 : 606) [*Armadillo feae*]

SYNTYPES : two males. Reg. no. 1921:10:18:2612. Tagata, Mt Mooleyit, Tenasserim, Burma. 5000–6000 m. March 1887. Collected by L. Fea. Budde-Lund Collection.

galeatus (Budde-Lund) (1895 : 605) [*Armadillo galeatus*]

SYNTYPES : one male ; one other specimen in fragments. Reg. no. 1921:10:18:2613. Bhamo, Burma. July 1886. Collected by L. Fea. Budde-Lund Collection.

marcidus (Budde-Lund) (1904 : 117) [*Armadillo marcidus*]

HOLOTYPE : male. Reg. no. 1921:10:18:2614. Pulo, Penang I., Malaysia. c. 700 m. February 1897. Collected by L. Fea and Loria. Budde-Lund Collection.

POLYACANTHUS Budde-Lund

transvaalensis Barnard (1932 : 321)

SYNTYPE : female. Reg. no. 1933:1:25:418–419. Zoutlansberg, Transvaal. Collected by R. F. Lawrence. Presented by the South African Museum.

REDUCTONISCUS Kesselyák

fritschei Verhoeff (1937a : 415)

SYNTYPES : three females. Reg. no. 1937:7:6:151–153. Berlin, East Germany. Collected by H. Fritsche. Purchased from K. W. Verhoeff.

SAIDJAHUS Budde-Lund

altimontis Jackson (1936 : 83)

SYNTYPES : one male ; one female. Reg. no. 1938:5:23:3–4. Pakka, North Borneo. 10 000 ft. 25.3.1929. Presented by R. E. W. Vallentin.

creper Budde-Lund (1904 : 49)

SYNTYPES : three males ; eight females. Reg. no. 1921:10:18:939–949. Telang and Pagat, Borneo. Collected by Grabowski. Budde-Lund Collection.

SPHERILLO Dana

ambitiosus (Budde-Lund) (1885 : 34) [*Armadillo ambitiosus*]

SYNTYPES : two males ; one female. Reg. no. 1921:10:18:801–803. New Zealand. Budde-Lund Collection.

bicoloratus (Budde-Lund) (1895 : 602) [*Armadillo bicoloratus*]

SYNTYPES : one male ; four females ; one other specimen in fragments. Reg. no. 1921:10:18:808–813. Mt Carin, Aseinii Cheba, Burma. 1200–1300 m. January 1880. Collected by L. Fea. Budde-Lund Collection.

bifrons (Budde-Lund) (1885 : 38) [*Armadillo bifrons*]

SYNTYPES : six males ; two females. Reg. no. 1921:10:18:814–821. Rockhampton, Queensland, Australia. Collected by M. Salmin. Budde-Lund Collection.

SYNTYPE : female. Reg. no. 1956:10:10:118. Rockhampton, Queensland, Australia. Collected by Salmin. Presented by University College, Dundee.

brachycephalus Budde-Lund (1904 : 84)

HOLOTYPE (?) : fragments. Reg. no. 1921:10:18:824. Pagat, Borneo, Indonesia. Collected by Grabowski. Budde-Lund Collection.

caligans Budde-Lund (1904 : 92)

SYNTYPE : female. Reg. no. 1921:10:18:826. Bohol I., Philippine Is. Collected by Prof. A. Sempler. Budde-Lund Collection.

decoratus Budde-Lund (1904 : 81)

SYNTYPE : fragments. Reg. no. 1921:10:18:841. Thailand. Budde-Lund Collection.

SYNTYPES : two females. Reg. no. 1921:10:18:842–843. Koh-Chang I., Thailand. Collected by T. Mortensen. Budde-Lund Collection.

dispersus Budde-Lund (1904 : 70)

SYNTYPES : two males. Reg. no. 1921:10:18:844–845. Botanical Gardens, Hamburg. 'Among plants from Bismark Archipelago, Solomon Is.' Collected by L. Reh. Budde-Lund Collection.

erinaceus (Budde-Lund) (1885 : 36) [*Armadillo erinaceus*]

SYNTYPES : two females. Reg. no. 1921:10:18:847–848. Upolu I., Samoa, Pacific Ocean. Budde-Lund Collection.

frontalis (Dollfus) (1900 : 522) [nom. nov. for *Armadillo danae* Budde-Lund 1904 : 67]
SYNTYPES : two males. Reg. no. 1904:11:5:11–12. Makaweli, Kauai I., Hawaiian Is. 3000 ft. 1897. Presented by the Joint Committee for Investigating the Fauna of the Sandwich Islands.

grisescens Budde-Lund (1902 : 380)
SYNTYPES : one male ; three females. Reg. no. 1921:10:18:849–852. Aring, Kelantan, Malaysia. Collected by the Skeat Expedition. Budde-Lund Collection.

grossus (Budde-Lund) (1885 : 19) [*Armadillo grossus*]
SYNTYPES : eight females. Reg. no. 1921:10:18:853–859. Rockhampton, Queensland, Australia. Budde-Lund Collection.
SYNTYPES : one male ; one female. Reg. no. 1956:10:10:119–120. Rockhampton, Queensland, Australia. Presented by University College, Dundee.

hebridarum Verhoeff (1926b : 297)
SYNTYPE : female. Reg. no. 1928:7:4:18. New Hebrides, Pacific Ocean. Collected by F. Speiser. Purchased from K. W. Verhoeff.

hypotoreus Jackson (1936 : 84)
SYNTYPES : two females. Reg. no. 1938:5:23:5–8. Pakka, North Borneo, 10 000 ft. 23.3.1929. Presented by the Raffles Museum.

ingens Budde-Lund (1904 : 91)
HOLOTYPE : fragments. Reg. no. 1921:10:18:863. Bohol I., Philippines. Collected by Semper. Budde-Lund Collection.

lentus Budde-Lund (1904 : 88)
SYNTYPES : one male ; two females ; one other specimen in fragments. Reg. no. 1921:10:18:867–870. New Guinea. 1894. Collected by L. Loria. Budde-Lund Collection.

maculosus Budde-Lund (1904 : 80)
HOLOTYPE : male. Reg. no. 1921:10:18:872. Silhouette I., Seychelle Is., Indian Ocean. Collected by A. Brauer. Budde-Lund Collection.

marginatus Budde-Lund (1904 : 65)
HOLOTYPE : female. Reg. no. 1921:10:18:873. Auckland, New Zealand. Collected by Suter. Budde-Lund Collection.

marquesarum Jackson (1933 : 156) [*Spherillo* (*Xestodillo ?*) *marquesarum*]
SYNTYPES : one male ; three females. Reg. no. 1933:12:20:7–10. Teavanui, Uapou, Marquesan Is. 2900 ft. 27.12.1931. Collected by Le Bronnec. Presented by H. G. Jackson.

montivagus (Budde-Lund) (1885 : 35) [*Armadillo montivagus*]
SYNTYPES : two males. Reg. no. 1921:10:18:874 & 877. Upola Is. Budde-Lund Collection.
SYNTYPES : one male ; one female. Reg. no. 1956:10:10:138–139. Upola I., Samoan Is. Presented by University College, Dundee.

nicobaricus (Budde-Lund) (1885 : 31) [*Armadillo nicobaricus*]
HOLOTYPE : male (fragment only). Reg. no. 1921:10:18:878. 'Pulo Milu', Nicobar I., Bay of Bengal. Collected by the Galathea Expedition. Budde-Lund Collection.

nobilis Budde-Lund (1904 : 90)
HOLOTYPE (?) : female. Reg. no. 1921:10:18:879. Oshima, Riu Kiu Is., nr Okinawa Is. Budde-Lund Collection.

obliquipes Budde-Lund (1904 : 85)
HOLOTYPE (?) : female. Reg. no. 1921:10:18:880. Bohol I., Philippine Is. Collected by Semper. Budde-Lund Collection.

parvus (Budde-Lund) (1885 : 25) [*Armadillo parvus*]
SYNTYPES : two males. Reg. no. 1921:10:18:892–893. Silhouette, Seychelle Is., Indian Ocean. Collected by Mobia. Budde-Lund Collection.

peltatus Budde-Lund (1904 : 78)
SYNTYPES : one male ; one female. Reg. no. 1921:10:18:906–907. Seychelle Is., Indian Ocean. Collected by A. Brauer. Budde-Lund Collection.

perkinsi (Dollfus) (1900 : 522) [*Armadillo perkinsi*]

HOLOTYPE : male. Reg. no. 1904:11:5:10. Haleakala, Kauai I., Hawaiian Is. 5000 ft. April 1894. Collected by Perkins. Presented by the Joint Committee for Investigating the Fauna of the Sandwich Islands.

purpurascens Budde-Lund (1913b : 371)

HOLOTYPE (?) : female. Reg. no. 1921:10:18:908. Isle of Pines, New Caledonia, Pacific Ocean. Collected by the 'Sealark' Expedition. Budde-Lund Collection.

rufomarginatus Budde-Lund (1904 : 64)

HOLOTYPE : female. Reg. no. 1921:10:18:909. Taranga, New Zealand. Collected by Dr Thilenius. Budde-Lund Collection.

rugulosus (Miers) (1876 : 225) [*Cubaris rugulosus*]

SYNTYPES : male ; female ; two other specimens in fragments (dry). Reg. no. 1845:61. New Zealand. Presented by Dr A. Sinclair.

setaceus Budde-Lund (1904 : 89)

HOLOTYPE : female. Reg. no. 1921:10:18:924. Auckland, New Zealand. Budde-Lund Collection.

sollers Budde-Lund (1904 : 55)

HOLOTYPE : female. Reg. no. 1921:10:18:925. Rockhampton, Queensland, Australia. Budde-Lund Collection.

spicatus Jackson (1927 : 4)

SYNTYPES : three males ; thirteen females. Reg. no. 1928:3:8:11–20. Malololelei, Upola, Samoan Is., Pacific Ocean. 2000 ft. 25.4.1924. Collected and presented by P. A. Buxton and G. H. E. Hopkins.

SYNTYPES : two males ; four females. Reg. no. 1952:4:18:125–128. Malololelei, Upola, Samoan Is. Collected by Buxton and Hopkins. Jackson Collection.

tarangensis Budde-Lund (1904 : 67)

SYNTYPES : one male ; one female. Reg. no. 1921:10:18:926. Taranga I., New Zealand. Budde-Lund Collection.

weberi (Dollfus) (1907 : 364) [*Armadillo weberi*]

SYNTYPE : male. Reg. no. 1921:10:18:1672. Ngalau Cave, nr Pajakomboh, Sumatra. Collected by M. Weber. Budde-Lund Collection.

SYNARMADILLO Dollfus

clausus Dollfus (1892a : 388)

SYNTYPE : female. Reg. no. 1921:10:18:1360. Assinie, Ivory Coast, West Africa. (Locality given on label : Habessinia.) Collected by C. Alluaud. Budde-Lund Collection.

globus Budde-Lund (1908 : 276)

SYNTYPES : two males ; one female. Reg. no. 1921:10:18:1376–1378. Cameroons, West Africa. Collected by J. Sjostedt. Budde-Lund Collection.

SYNTYPES : four males ; eight females. Reg. no. 1921:10:18:1364–1375. Cameroons, West Africa. Collected by S. Sjostedt. Budde-Lund Collection.

marmoratus Budde-Lund (1910 : 15)

SYNTYPES : ten males ; fourteen females. Reg. no. 1921:10:18:1380–1391. Rain forest at Kibongoto, Kilimanjaro, Tanganyika ; rain forest at Meru, Tanganyika. Collected by Y. Sjostedt. Budde-Lund Collection.

SYNTYPES : three females. Reg. no. 1921:10:18:1392–1394. Rain forest at Kibongoto, Kilimanjaro, Tanganyika. Budde-Lund Collection.

nigropunctatus (Hilgendorf) (1893 : 154) [*Periscyphis nigropunctatus*]

SYNTYPES : two males ; four females. Reg. no. 1921:10:18:1395–1400. Togo, West Africa. Collected by Büttner. Budde-Lund Collection.

pygmaeus (Budde-Lund) (1898 : 6) [*Periscyphis pygmaeus*]

SYNTYPE : female (?) (fragments). Reg. no. 1921:10:18:1401. Runsoro. Collected by Pasch and Stuhlmann. Budde-Lund Collection.

simplex Budde-Lund (1910 : 16)

Syntypes : three females. Reg. no. 1921:10:18:1402–1404. Kibongoto, Kilimanjaro, Tanganyika. 'In leaf mould.' November 1905. Collected by Y. Sjostedt. Budde-Lund Collection.

VENEZILLO Verhoeff

dumorum (Dollfus) (1896c : 391) [*Armadillo dumorum*]

Syntypes : two males ; three females. Reg. no. 1896:1:11:26–27. Mustique I., Windward Is., West Indies. 'June. Beating bushes.' 1889–91. Collected by H. H. Smith. Presented by the West India Committee.

grenadensis (Budde-Lund) (1893 : 115) [*Armadillo grenadensis*]

Syntype : male. Reg. no. 1921:10:18:1122. Grenada, Windward Is., West Indies. May 1891. Collected by Meinert. Budde-Lund Collection.

pumilus (Budde-Lund) (1893 : 115) [*Armadillo pumilus*]

Syntype : female (fragments). Reg. no. 1921:10:18:1136. Venezuela. 1891. Collected by Meinert. Budde-Lund Collection.

truncorum (Budde-Lund) (1893 : 116) [*Armadillo truncorum*]

Syntype : fragments. Reg. no. 1921:10:18:1167. Venezuela. Budde-Lund Collection.

Syntypes : three males ; one female. Reg. no. 1956:10:10:126–129. Caracas, Venezuela. Presented by University College, Dundee.

venustus (Budde-Lund) (1893 : 114) [*Armadillo venustus*]

Syntypes : one male ; six females. Reg. no. 1921:10:18:1169–1174. La Moka, Venezuela. August 1891. Collected by Meinert. Budde-Lund Collection.

Syntype : female. Reg. no. 1956:10:10:123. La Moka, Venezuela. August 1891. Collected by Meinert. Presented by University College, Dundee.

INCERTAE SEDIS

KISUMA Budde-Lund

papillosa Budde-Lund (1912b : 169)

Syntypes : one male ; one female. Reg. no. 1921:10:18:5139–5140. Semarang, Java, Indonesia. December 1909. Collected by E. Jacobson. Budde-Lund Collection.

OURACHAERUS Kinahan

caudatus Kinahan (1859 : 198)

Holotype : posterior segments missing (dry). Reg. no. 1973:514:1. Locality and donor unknown.

PYRGONISCUS Kinahan

cinctutus Kinahan (1859 : 200)

Holotype : female (dry). Reg. no. 1856:85. Eastern Seas. Collected during the voyage of H.M.S. 'Herald'. Donor unknown.

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APPENDIX 1

The Collection also contains a large number of specimens labelled as types, mostly from the Budde-Lund Collection, for which no reference can be found in published literature. It seems possible that these are specimens with manuscript names which have been incorporated into personal collections but which have never been published. A list of this material comprising 167 items is given below; and a list of the manuscript names has been deposited in the library of the British Museum (Natural History).

Family **PORCELLIONIDAE**

Agabiforius sp.
Three specimens. Reg. no. 1921:10:18:4066–4068. Fundo I., Zanzibar. 21.4.1903. Collected by C. W. Pemba (?). Budde-Lund Collection.

Hemilepistus sp.
Two specimens. Reg. no. 1921:10:18:4113–4114. Asia. Budde-Lund Collection.

Leptotrichus sp.
One specimen. Reg. no. 1921:10:18:3969. Zanzibar I. 20.5.1888. Collected by Struhlmann. Budde-Lund Collection.

Lucasius sp.
Five specimens. Reg. no. 1921:10:18:5177–5181. Philippeville. Budde-Lund Collection.

Metoponorthus sp.
One specimen. Reg. no. 1921:10:18:5224. Inca, Malorca. Budde-Lund Collection.

Metoponorthus sp.
One specimen. Reg. no. 1921:10:18:5238. Taurus, Cilicia, Turkey. Budde-Lund Collection.

Metoponorthus sp.
One specimen. Reg. no. 1921:10:18:5246. Corral, Chile. Budde-Lund Collection.

Metoponorthus sp.
Two specimens. Reg. no. 1921:10:18:5288–5289. Mt Grappa, Italy. Budde-Lund Collection.

Metoponorthus sp.
Three specimens. Reg. no. 1921:10:18:5290–5295. Boccadifalco, Italy. 17.2.1896. Collected by F. Silvestri. Budde-Lund Collection.

Metoponorthus sp.
Two specimens. Reg. no. 1921:10:18:5323–5324. East Africa. Collected by Gadat. Budde-Lund Collection.

Metoponorthus sp.

Six specimens. Reg. no. 1921:10:18:5369–5374. Gülek, Cilicia, Turkey. Budde-Lund Collection.

Metoponorthus sp.

One specimen. Reg. no. 1921:10:18:5488. Jerusalem, Israel. Budde-Lund Collection.

Metoponorthus sp.

Six specimens. Reg. no. 1921:10:18:5502–5507. Poizo. Budde-Lund Collection.

Porcellio sp.

One specimen. Reg. no. 1921:10:18:4241. Monchique, Portugal. 3.5.1888. Collected by Moller. Budde-Lund Collection.

Porcellio sp.

One specimen. Reg. no. 1921:10:18:3790. Algeria. Collected by E. Simon. Budde-Lund Collection.

Porcellio sp.

One specimen. Reg. no. 1921:10:18:4259. Asia Minor. Budde-Lund Collection.

Porcellio sp.

One specimen. Reg. no. 1925:7:452. Siebenburgen. Koch Collection.

Porcellio sp.

Four specimens. Reg. no. 1921:10:18:4280–4283. Sa. do Gerez Mts, Portugal. June 1899. Collected by Vicira. Budde-Lund Collection.

Porcellio sp.

One specimen. Reg. no. 1921:10:18:4287. Hercegowina. Budde-Lund Collection.

Porcellio sp.

One specimen. Reg. no. 1921:10:18:4982. Algeria. 'In monte Djebel-Mahid 2000 m inl. cortice Cedri 1885.' Collected by E. Simon. Budde-Lund Collection.

Porcellio sp.

Two specimens. Reg. no. 1921:10:18:4295–4296. Mauritius I., Indian Ocean. Collected by Dr Emmery. Budde-Lund Collection.

Porcellio sp.

Three specimens. Reg. no. 1891:11:15:1–3. Tsu-Shima. Collected by Holst. Determined/named by G. Budde-Lund. Purchased from H. Seebohm.

Porcellio sp.

Ten specimens. Reg. no. 1907:4:30:11–20. Rio de Oro, Morocco. February 1902. Collected by W. Riggenbach. Determined/named by G. Budde-Lund. Presented by W. Rothschild.

Five specimens. Reg. no. 1921:10:18:4361–4364. Rio de Oro, Sahara. Budde-Lund Collection.

Porcellio sp.

One specimen (dry). Reg. no. 1840:6:26:731. Cape of Good Hope. Purchased from Dr Krauss.

Porcellio sp.

Three specimens. Reg. no. 1931:4:27:58–60. Palestine. Purchased from K. W. Verhoeff.

Porcellio sp.

Five specimens. Reg. no. 1921:10:18:4420–4424. Tunis. 27.3.1896. Collected by F. Silvestri. Budde-Lund Collection.

Porcellio sp.

Two specimens. Reg. no. 1845:112. Norfolk I., Pacific Ocean. Presented by George Newport.

Two specimens (dry). Reg. no. 1856:105. Norfolk I., Pacific Ocean. June 1855. Collected during the voygage of H.M.S. 'Herald'. Donor unknown.

Porcellio sp.

Twelve specimens. Reg. no. 1921:10:18:4441–4452. Coimbra, Portugal. April 1896. Budde-Lund Collection.

Porcellio sp.
Four specimens. Reg. no. 1921:10:18:4462–4465. Naxos I., Greece. Budde-Lund Collection.

Porcellio sp.
Three specimens. Reg. no. 1921:10:18:3900–3902. Biskra, Algeria. Budde-Lund Collection.

Porcellio sp.
Two specimens. Reg. no. 1921:10:18:4501–4502. Japan. Collected by Hilgendorf. Budde-Lund Collection.

Porcellio sp.
Two specimens. Reg. no. 1921:10:18:3904–3905. Jebel Tarhuna Mts, Libya. Budde-Lund Collection.

Porcellio sp.
One specimen. Reg. no. 1921:10:18:5153. Santorin. Budde-Lund Collection. Three specimens. Reg. no. 1921:10:18:5154–5156. Favorita. Collected by Silvestri. Budde-Lund Collection.

Porcellio sp.
Four specimens. Reg. no. 1921:10:18:5157–5160. Palermo, Italy. Budde-Lund Collection.

Porcellio sp.
One specimen. Reg. no. 1921:10:18:4599. Cansiglio. Budde-Lund Collection.

Porcellio sp.
One specimen (dry). Reg. no. 1973:480:1. Locality and donor unknown.

Porcellio sp.
One specimen. Reg. no. 1921:10:18:4887. Algeria. Collected by Beresford. Budde-Lund Collection.

Porcellio sp.
Five specimens (dry). Reg. no. 1845:49. New South Wales, Australia. Purchased from Mr Wood.

Porcellio sp.
Three specimens (dry). Reg. no. 1973:481:3. Tristan d'Acunha. Presented by Captain Carmichael.

Porcellio sp.
Four specimens. Reg. no. 1921:10:18:4948–4951. Liguria, Italy. September 1897. Collected by G. Mantero. Budde-Lund Collection.

Uramba sp.
One specimen. Reg. no. 1921:10:18:4069. No locality. Budde-Lund Collection.

Uramba sp.
Three specimens. Reg. no. 1921:10:18:4081–4083. Kibwezi, Kenya. Budde-Lund Collection.

Uramba sp.
One specimen. Reg. no. 1921:10:18:4084. Gansilla, East Africa. Budde-Lund Collection.

Family **TRACHELIPIDAE**

Nagurus sp.
Six specimens. Reg. no. 1921:10:18:5741–5746. Japan. Collected by Hilgendorf. Budde-Lund Collection.

Nagurus sp.
Five specimens. Reg. no. 1921:10:18:1486–1490. Koh-Kahdat. 9.1.1900. Collected by 'Th. Mort.' Budde-Lund Collection.

Phalaba sp.
One specimen. Reg. no. 1921:10:18:2104. East Africa. Budde-Lund Collection.
Two specimens. Reg. no. 1921:10:18:2105–2106. Amani, Tanganyika. Collected by Vosseler. February 1905. Budde-Lund Collection.

Phalaba sp.

One specimen. Reg. no. 1921:10:18:2107. Ukinga. Budde-Lund Collection.

Phalaba sp.

Two specimens. Reg. no. 1921:10:18:2108–2109. Amani, Tanganyika. Budde-Lund Collection.

Family **ARMADILLIDIIDAE**

Armadillidium sp.

Three specimens. Reg. no. 1921:10:18:2683–2685. Hamman Meskhoutin. Budde-Lund Collection.

Twelve specimens. Reg. no. 1921:10:18:2686–2689. Constantine, Algeria. 23.3.1901. Collected by M. Kraepelin. Budde-Lund Collection. Three specimens. Reg. no. 1921:10:18:2698–2700. Algier. Budde-Lund Collection.

Armadillidium sp.

One specimen. Reg. no. 1921:10:18:2701. Stora, Sweden. Collected by E. Simon. Budde-Lund Collection.

Armadillidium sp.

One specimen. Reg. no. 1921:10:18:2702. Ainos, Kefallinia I., Greece. Collected by E. von Oertzen. Budde-Lund Collection.

Armadillidium sp.

Two specimens. Reg. no. 1921:10:18:2703–2704. Cyrenaica, Libya. Budde-Lund Collection.

Armadillidium sp.

One specimen. Reg. no. 1921:10:18:2712. Tunis, Tunisia. Budde-Lund Collection.

Armadillidium sp.

Six specimens. Reg. no. 1921:10:18:2714–2719. Louk el Arba. Collected by Silvestri. Budde-Lund Collection.

One specimen. Reg. no. 1921:10:18:2720. Baboneh. Collected by Silvestri. Budde-Lund Collection.

Armadillidium sp.

Two specimens. Reg. no. 1921:10:18:2791–2792. Algiers. Collected by de Gaulle. Budde-Lund Collection.

Five specimens. Reg. no. 1921:10:18:2793–2797. Sidi Bel Akaren. Collected by F. Silvestri. Budde-Lund Collection.

Armadillidium sp.

Twelve specimens. Reg. no. 1921:10:18:2842–2853. San Cataldo. Italy. 1898. Collected by Dr Peracca. Budde-Lund Collection.

Armadillidium sp.

Seven specimens. Reg. no. 1921:10:18:2936–2942. Santa Ninfa, Sicily. 15.3.1896. Collected by F. Silvestri. Budde-Lund Collection.

Armadillidium sp.

One specimen. Reg. no. 1921:10:18:2943. Santa Ninfa, Sicily. Collected by F. Silvestri. Budde-Lund Collection.

Armadillidium sp.

Five specimens. Reg. no. 1921:10:18:2962–2966. Tunis. 27.3.1896. Budde-Lund Collection.

Armadillidium sp.

One specimen (dry). Reg. no. 1973:479:1. Sierra Leone. Presented by the Rev. D. S. Morgan.

Armadillidium sp.

Two specimens. Reg. no. 1921:10:18:2980–2981. Baboneh. Collected by F. Silvestri. Budde-Lund Collection.

Armadillidium sp.

One specimen. Reg. no. 1921:10:18:2982. Capella de S. Antonio (Finalborge). 4.3.1898. Collected by R. Gestro. Budde-Lund Collection.

Armadillidium sp.

Two specimens. Reg. no. 1921:10:18:2983–2984. Ulai (?). Budde-Lund Collection.

Armadillidium sp.

One specimen. Reg. no. 1921:10:18:2985. Ainos, Kefallina, Greece. Collected by E. von Oertzen. Budde-Lund Collection.

Armadillidium sp.

Six specimens. Reg. no. 1921:10:18:2986–2991. Palmi, Italy. 17.5.1893. Scilla, Italy. 24.6.1893. Collected by H. J. Hansen. Budde-Lund Collection.

Armadillidium sp.

One specimen. Reg. no. 1921:10:18:5849. Asia Minor. Collected by Dr Th. Krsyser. (Mus. Berlin.) Budde-Lund Collection.

Armadillidium sp.

Two specimens. Reg. no. 1921:10:18:2993–2994. Corfu I. Budde-Lund Collection.

Armadillidium sp.

One specimen. Reg. no. 1921:10:18:3022. Malosin. 5.8.1902. Collected by Mrazek. Budde-Lund Collection.

Three specimens. Reg. no. 1921:10:18:3023–3025. Danilov Grad, Yugoslavia. Collected by Mrazek. Budde-Lund Collection.

Twelve specimens. Reg. no. 1921:10:18:3026–3037. Celinje, Yugoslavia. Collected by Mrazek. Budde-Lund Collection.

Armadillidium sp.

Three specimens. Reg. no. 1921:10:18:3082–3084. Zadar (Zara), Yugoslavia. Collected by A. Dollfus. Budde-Lund Collection.

Armadillidium sp.

One specimen. Reg. no. 1921:10:18:3085. Eaux Counet, Pyrénées. Collected by Seidtl. Budde-Lund Collection.

Armadillidium sp.

Two specimens. Reg. no. 1956:10:10:135–136. Key West, Florida, USA. Presented by University College, Dundee (ex Budde-Lund Collection).

Armadillidium sp.

One specimen. Reg. no. 1921:10:18:3153. Corfu I. Collected by Gracia (?). Budde-Lund Collection.

Five specimens. Reg. no. 1921:10:18:3154–3158. Atri, Italy. Collected by F. Silvestri. Budde-Lund Collection.

Armadillidium sp.

One specimen. Reg. no. 1921:10:18:3159. Dalmatia, Yugoslavia. Budde-Lund Collection.

Armadillidium sp.

Three specimens. Reg. no. 1921:10:18:3160–3162. Meleda (?), Yugoslavia. 13.8.1880. Budde-Lund Collection.

Armadillidium sp.

One specimen. Reg. no. 1921:10:18:3163. Corsica. Collected by E. Simon. Budde-Lund Collection.

Armadillidium sp.

Two specimens. Reg. no. 1921:10:18:3185–3186. Roumania. Collected by Jaquet. Budde-Lund Collection.

Armadillidium sp.

c. sixty specimens. Reg. no. 1921:10:18:3187–3210. Njegos, Montenegro, Yugoslavia. Collected by Mrazek. Budde-Lund Collection.

Six specimens. Reg. no. 1921:10:18:3211–3216. Podgornica (now Titograd), Yugoslavia. Collected by Mrazek. Budde-Lund Collection.

Armadillidium sp.
Five specimens. Reg. no. 1921:10:18:3217–3221. Yugoslavia. Budde-Lund Collection.

Armadillidium sp.
Three specimens. Reg. no. 1921:10:18:3223–3225. Zaragoza (Saragossa), Spain. Budde-Lund Collection.

Armadillidium sp.
Two specimens. Reg. no. 1921:10:18:3226–3227. Flumentorgne. Budde-Lund Collection.

Armadillidium sp.
Five specimens. Reg. no. 1921:10:18:3241–3245. Brescia, Italy. Budde-Lund Collection.

Armadillidium sp.
Three specimens. Reg. no. 1921:10:18:3246–3248. Spezia, Italy. Budde-Lund Collection.

Armadillidium sp.
One specimen. Reg. no. 1921:10:18:3264. Yugoslavia. Collected by Uljanin. Budde-Lund Collection.

Armadillidium sp.
Seven specimens. Reg. no. 1921:10:18:3275–3281. Bocadifalco, Italy. 17.2.1896. Collected by F. Silvestri. Budde-Lund Collection.

Twenty-two specimens. Reg. no. 1921:10:18:3265–3278 & 3282–3287. Bivona, Sicily. February 1896. Collected by F. Silvestri. Budde-Lund Collection.

Armadillidium sp.
One specimen. Reg. no. 1921:10:18:3296. Kieff (Kiyev), Ukraine, USSR. Collected by Uljanin. Budde-Lund Collection.

Four specimens. Reg. no. 1921:10:18:3297–3301. Sympheropolis. Collected by Uljanin. Budde-Lund Collection.

Armadillidium sp.
Two specimens. Reg. no. 1921:10:18:3302–3303. Sympheropolis. Collected by Uljanin. Budde-Lund Collection.

Armadillidium sp.
Six specimens. Reg. no. 1895:1:24:41–46. Cettinje. Named/determined by G. Budde-Lund. Presented by Dr Werner.

Armadillidium sp.
Four specimens. Reg. no. 1921:10:18:3312–3315. Carthajine. Collected by F. Silvestri. Budde-Lund Collection.

Ten specimens. Reg. no. 1921:10:18:3316–3325. Tabarka, Tunisia. 2.8.1896. Collected by F. Silvestri. Budde-Lund Collection.

Five specimens. Reg. no. 1921:10:18:3326–3330. Tunis, Tunisia. 27.3.1896. Collected by Silvestri. Budde-Lund Collection.

Five specimens. Reg. no. 1921:10:18:3331–3334. Baboneh. Budde-Lund Collection.

Eluma sp.
Three specimens. Reg. no. 1921:10:18:3760–3761. Oran, Algeria. May 1883. Collected by E. Simon. Budde-Lund Collection.

Toradjia sp.
One specimen. Reg. no. 1921:10:18:1660. Ceylon. Budde-Lund Collection.

Toradjia sp.
One specimen. Reg. no. 1921:10:18:1661. East Java. Budde-Lund Collection.

Family **EUBELIDAE**

Eubelum sp.
One specimen. Reg. no. 1907:5:6:15. Roromo, Ukinga Forest. 7700 ft. Named/determined by G. Budde-Lund. Presented by R. Cowestay (? or Crawshay).

One specimen. Reg. no. 1921:10:18:588. Nawobi (? probably Nairobi). Budde-Lund Collection.

Eubelum sp.
Four specimens. Reg. no. 1921:10:18:591–594. Gardulla, Ethiopia. Budde-Lund Collection.
Eubelum sp.
Two specimens. Reg. no. 1921:10:18:595–596. S. Kaffa, Ethiopia. Budde-Lund Collection.
Eubelum sp.
Three specimens. Reg. no. 1921:10:18:614–616. Ethiopia. Budde-Lund Collection.
Eubelum sp.
One specimen. Reg. no. 1921:10:18:617. Kaffa, Ethiopia. Budde-Lund Collection.
Eubelum sp.
One specimen. Reg. no. 1921:10:18:618. San Salvador. Budde-Lund Collection.
Eubelum sp.
One specimen. Reg. no. 1921:10:18:626. Kaffa, Ethiopia. Budde-Lund Collection.
Eubelum sp.
Twelve specimens. Reg. no. 1921:10:18:627–638. Gardulla, Ethiopia. 2500–2800 m. 13.1.1901. Collected by O. Neumann. Budde-Lund Collection.
Mesarmadillo sp.
One specimen. Reg. no. 1921:10:18:729. Niger Delta, W. Africa. Budde-Lund Collection.
Mesarmadillo sp.
One specimen. Reg. no. 1921:10:18:730. East Africa. Budde-Lund Collection.
Mesarmadillo sp.
One specimen. Reg. no. 1921:10:18:731. East Africa. Budde-Lund Collection.
Mesarmadillo sp.
One specimen. Reg. no. 1921:10:18:732. East Africa. Budde-Lund Collection.
Microcercus sp.
Four specimens. Reg. no. 1921:10:18:1230–1233. Bissao. Collected by H. Ehrhardt (Mus. Hamburg). Budde-Lund Collection.
Microcercus sp.
Two specimens. Reg. no. 1921:10:18:1268–1269. Langenburg, W. Germany. 27.4.1898. Collected by Fullborn. Budde-Lund Collection.
Microcercus sp.
Two specimens. Reg. no. 1893:11:9:9–10. Woods near Ngatana. Named/determined by G. Budde-Lund. Collected and presented by J. A. Gregory.
Microcercus sp.
Four specimens. Reg. no. 1921:10:18:1270–1273. Nakuru, Kenya. Collected by C. Alluaud. Budde-Lund Collection.
Microcercus sp.
Eight specimens. Reg. no. 1902:12:4:8–15. Cheradguea Mts and its slopes, Nyasaland. July and August 1895. Collected by A. Whyte. Named/determined by G. Budde-Lund. Presented by H. H. Johnston.
Eleven specimens. Reg. no. 1921:10:18:1274–1284. Nyasaland. Budde-Lund Collection.
Periscyphis sp.
One specimen. Reg. no. 1921:10:18:1303. East Africa. Budde-Lund Collection.
Periscyphis sp.
Five specimens. Reg. no. 1921:10:18:1304–1308. Ethiopia. Budde-Lund Collection.
Periscyphops sp.
One specimen. Reg. no. 1921:10:18:745. Africa. Budde-Lund Collection.
Periscyphops sp.
Two specimens. Reg. no. 1921:10:18:746–747. Shoa, Ethiopia. Budde-Lund Collection.
Periscyphops sp.
One specimen. Reg. no. 1921:10:18:748. No locality. Budde-Lund Collection.
Periscyphops sp.
One specimen. Reg. no. 1921:10:18:754. East Africa. Budde-Lund Collection.

Periscyphops sp.
Three specimens. Reg. no. 1921:10:18:757–759. S. Kaffa, Ethiopia. Budde-Lund Collection.

Periscyphops sp.
Four specimens. Reg. no. 1921:10:18:764–767. Niger delta at Wari. Budde-Lund Collection.

Periscyphops sp.
One specimen (in fragments). Reg. no. 1921:10:28:768. Misahöhe, West Africa. Collected by Baumann, Budde-Lund Collection.

Family **SPHAERONISCIDAE**

Scleropactes sp.
Five specimens. Reg. no. 1921:10:18:956–960. Ecuador. Budde-Lund Collection.

Scleropactes sp.
Two specimens. Reg. no. 1921:10:18:965–967. Ecuador. Budde-Lund Collection.

Sphaeroniscus sp.
One specimen (in fragments). Reg. no. 1921:10:18:2215. Bogota, Colombia. Collected by Burger. Budde-Lund Collection.

Sphaeroniscus sp.
Three specimens. Reg. no. 1921:10:18:2216–2218. Costa Rica, South America. Budde-Lund Collection.

Sphaeroniscus sp.
One specimen (in fragments). Reg. no. 1921:10:18:2219. Bogota, Colombia. Collected by Burger. Budde-Lund Collection.

Sphaeroniscus sp.
One specimen (in fragments). Reg. no. 1921:10:18:2220. Peru. Budde-Lund Collection.

Sphaeroniscus sp.
One specimen. Reg. no. 1921:10:18:2221. Paramaribo, Surinam, South America. Budde-Lund Collection.
Four specimens. Reg. no. 1921:10:18:2222–2225. Ecuador. Budde-Lund Collection.

Sphaeroniscus sp.
Six specimens. Reg. no. 1921:10:18:2226–2231. Venezuela. Budde-Lund Collection.

Family **ARMADILLIDAE**

Adinda sp.
Two specimens. Reg. no. 1921:10:18:1665–1666. Singapore. Collected by H. N. Ridley. Budde-Lund Collection.

Adinda sp.
One specimen. Reg. no. 1921:10:18:1667. Sicbolangst (?). Collected by Jachan (?). Budde-Lund Collection.

Adinda sp.
Two specimens. Reg. no. 1921:10:18:1668–1669. Singapore. 1898. Collected by H. N. Ridley. Budde-Lund Collection.

Adinda sp.
One specimen (in fragments). Reg. no. 1921:10:18:1670. Sumatra. Budde-Lund Collection.

Adinda sp.
One specimen. Reg. no. 1921:10:16:1671. Pulo Penang, Burma. February 1879. Collected by Fea and Loria. Budde-Lund Collection.

Armadillo sp.
Two specimens. Reg. no. 1921:10:18:2462–2463. Ceylon. Budde-Lund Collection.

Armadillo sp.
Four specimens. Reg. no. 1921:10:18:2421–2424. South West Australia. Budde-Lund Collection.

Armadillo sp.

One specimen. Reg. no. 1893:12:15:1–8 (part). North Clin Hills, Upper Burma. Named/determined by G. Budde-Lund. Presented by E. G. Watson.

Armadillo sp.

One specimen (dry). Reg. no. 1842:22. Philippine Is. Purchased from Mr Cuming.

Armadillo sp.

One specimen. Reg. no. 1921:10:18:2516. Hackgall, Ceylon. Collected by A. Willey. Budde-Lund Collection.

One specimen. Reg. no. 1907:4:30:22. Hackgall, Ceylon. January 1906. Named/determined by G. Budde-Lund.

Bethalus sp.

Three specimens. Reg. no. 1921:10:18:1185–1187. Fort Dauphin, Madagascar. Budde-Lund Collection.

Bethalus sp.

One specimen. Reg. no. 1921:10:18:1188. Fort Dauphin, Madagascar. Budde-Lund Collection.

Bethalus sp.

Two specimens. Reg. no. 1921:10:18:1202–1203. Fort Dauphin, Madagascar. Budde-Lund Collection.

Bethalus sp.

Nine specimens. Reg. no. 1921:10:18:1209–1217. Fort Dauphin, Madagascar. Budde-Lund Collection.

Diploexochus sp.

One specimen (in fragments). Reg. no. 1921:10:18:1088. Uvinza, Tanganyika. 16.12.1896. Collected by H. Fremann. Budde-Lund Collection.

Diploexochus sp.

Thirteen specimens. Reg. no. 1921:10:18:1154–1166. Anjouan I., Madagascar. Budde-Lund Collection.

Sperillo sp.

Three specimens. Reg. no. 1921:10:18:804–806. Tonkin, Montes Mauson. 2000–3000 ft. Collected by H. Fruhstorfer. Budde-Lund Collection.

Sperillo sp.

Two specimens. Reg. no. 1921:10:18:822–823. Rio de Janeiro, Brazil. Budde-Lund Collection.

Sperillo sp.

One specimen. Reg. no. 1921:10:18:825. Tonkin, Montes Mauson. Collected by H. Fruhstorfer. Budde-Lund Collection.

Spherillo sp.

Fifteen specimens. Reg. no. 1921:10:18:829–840. California, USA. Collected by G. Eisen. Budde-Lund Collection.

Spherillo sp.

One specimen. Reg. no. 1921:10:18:846. Honolulu, Hawaii. 1874. Collected by d'Albertin. Budde-Lund Collection.

Spherillo sp.

Three specimens. Reg. no. 1921:10:18:1405–1407. Togo. Collected by Dr Büttner. Budde-Lund Collection.

INCERTAE SEDIS

Genus 1

Species *a*

One specimen. Reg. no. 1921:10:18:796. Uvinza, Tanganyika. Budde-Lund Collection.

Genus 2

Species *a*

One specimen. Reg. no. 1921:10:18:794. Shoa district, Ethiopia. Budde-Lund Collection.

Genus 3
Species *a*
One specimen. Reg. no. 1921:10:18:5704. Asia Minor. 23.10.1900. Budde-Lund Collection.
Species *b*
Two specimens. Reg. no. 1921:10:18:5701–5702. Genargentu. 26.1.1899. Collected by G. Doria. Budde-Lund Collection.
Genus 4
Species *a*
One specimen. Reg. no. 1921:10:18:5703. Sidi-Bel-Akaren, Algeria. Collected by F. Silvestri. Budde-Lund Collection.
Genus 5
Species *a*
Two specimens. Reg. no. 1921:10:18:797–798. South Shoa, Ethiopia. Budde-Lund Collection.
Genus 6
Species *a*
One specimen. Reg. no. 1921:10:18:5706. Paramaibo. Budde-Lund Collection.
Genus 7
Species *a*
One specimen (in fragments). Reg. no. 1921:10:18:799. Ruanda, East Africa. Budde-Lund Collection.
Genus 8
Species *a*
Fifteen specimens. Reg. no. 1921:10:18:5707–5721. Brasilia, Brazil. Budde-Lund Collection.
Species *b*
One specimen. Reg. no. 1921:10:18:5722. Rio de Janeiro, Brazil. Budde-Lund Collection.
Species *c*
Two specimens. Reg. no. 1921:10:18:5723–5724. Rio de Janeiro, Brazil. Budde-Lund Collection.
Genus 9
Species *a*
Three specimens. Reg. no. 1921:10:18:5726–5728. East Africa. Collected by Langeberg. Budde-Lund Collection.
Species *b*
One specimen. Reg. no. 1921:10:18:5725. Nyasa, Malawi. Budde-Lund Collection.
Genus 10
Species *a*
One specimen (in fragments). Reg. no. 1921:10:18:795. Shoa district, Ethiopia. 10.11.1900. Collected by Erlanger. Budde-Lund Collection.
Genus 11
Species *a*
One specimen. Reg. no. 1921:10:18:5747. Futschau. Budde-Lund Collection.
Species *b*
One specimen. Reg. no. 1921:10:18:5748. Tsing tua, Hong Kong. Budde-Lund Collection.
Species *c*
One specimen. Reg. no. 1921:10:5749. Japan. Collected by Hilgendorf. Budde-Lund Collection.
Genus 12
Species *a*
One specimen. Reg. no. 1921:10:18:800. Gardulla, Ethiopia. Budde-Lund Collection.

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CAMPYLASPIS SPECIES (CRUSTACEA: CUMACEA) FROM THE DEEP ATLANTIC

N. S. JONES

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BY

N. S. JONES k

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University of Liverpool
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CAMPYLASPIS SPECIES (CRUSTACEA : CUMACEA) FROM THE DEEP ATLANTIC

By N. S. JONES

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SYNOPSIS

Thirty-nine species of *Campylaspis* were collected during a number of cruises, mostly by ships of the Woods Hole Oceanographic Institution, in depths exceeding 200 m in the Atlantic between 1960 and 1969. Twenty-five of these are described as new. A key is included to the 98 species known at the time of writing.

INTRODUCTION

This paper deals with the genus *Campylaspis* (family Nannastacidae) from a number of collections made in the deep water of the Atlantic Ocean. Almost all the stations sampled were in depths exceeding 200 m and the great majority of samples were obtained by epibenthic sled dredges (Sanders & Hessler, 1969). Altogether 39 species of *Campylaspis* were collected, of which 25 are described here as new.

A preliminary account of the distribution of the Cumacea from several of these collections has been published (Jones & Sanders, 1972) and also descriptions of a number of new genera and species (Jones, 1973; Reyss, 1974). Reyss (1973) has also discussed the distribution of Cumacea in the deep waters of the Mediterranean.

The material studied was obtained during the following cruises:

Gay Head – Bermuda transect (Woods Hole Oceanographic Institution ships), 1960–69.

'Chain' cruise (WHOI) off Brazil, April 1973.

Dakar – Recife transect ('Atlantis II', WHOI), February 1967.

'Sarsia' cruise (Marine Biological Association) in Bay of Biscay, July 1967.

'Discovery' cruise (National Institute of Oceanography) near the Canary Islands, March 1968.

'Atlantis II' cruise (WHOI) Walvis Bay – Luanda, May 1968.

'Jean Charcot' cruise (Centre Océanologique de Bretagne) in North Atlantic, August–October 1969.

THE GENUS *CAMPYLASPIS*

Including those described in this paper there are now 98 species in the genus *Campylaspis* known to the author. In spite of this rather unwieldy number there seem to be no grounds at present for splitting the genus, but it may be divided into four main groups according to the sculpture or lack of it on the carapace, with two smaller groups of which one is rather miscellaneous. These are :

1. The *rubicunda*-group with the following 22 species :
   alba, nitens, nuda, orientalis, inornata, guttata, pacifica, pulchella, paeneglabra, mauritanica, rubicunda, laevigata, angularis, glabra, bonetti, amblyoda, rufa, kiiensis, thompsoni, similis, roscida, laticarpa.

   In this group the carapace is smooth, without lateral depressions, and with at most a pair of low rounded protuberances or with small granulations.
2. The *sulcata*-group with 20 species :
   striata, aulacoeis, fusiformis, porcata, canaliculata, granulata, tubulata, pumila, jonesi, latidactyla, sulcata, minor, legendrei, aperta, sticta, echinata, pilosa, redacta, cognata, unisulcata.

   In these there is a depression on either side of the carapace. If distinct ridges are present they do not extend to the dorsal hind end of the carapace. Some spines or a few low protuberances may be present but not conical, subcylindrical or rounded tubercles.
3. The *costata*-group with 24 species :
   platyuropus, uniplicata, vitrea, pileus, macrophthalma, hartae, sinuosa, undata, johnstoni, ovalis, arcuata, crispa, speciosa, costata, triplicata, umbensis, reticulata, paucispina, caperata, plicata, valleculata, exarata, mansa, bicarinata.

   These have one or more, usually two or three distinct ridges running horizontally or obliquely backwards on either side of the carapace, of which at least one extends onto the dorsum. Depressions may be present between the ridges but they are not defined posteriorly. Tubercles are not present.
4. The *verrucosa*-group with 24 species :
   affinis, serratipes, clavata, thetidis, maculata, sagamiensis, intermedia, horrida, submersa, rubromaculata, papillata, paucinodosa, horridoides, glebulosa, frigida, pustulosa, squamifera, torulosa, verrucosa, aspera, nodulosa, globosa, antarctica, multinodosa.

   These have moderate or large numbers of tubercles on the sides and dorsum of the carapace.
5. The *rostrata*-group with four species :
   rostrata, rostellata, aculeata, brevicornis.

   This is a small group in which the pseudorostrum is prominent and enlarged.
6. The *spinosa*-group with four species :
   spinosa, rupta, quadriplicata, bulbosa.

   These four species have little in common but do not fit into any other group.

The key which follows is based on that of Hale (1945) with some alterations, but is greatly enlarged to include more than twice the original number of species. The shape and markings of the carapace, including the eyelobe and the pseudorostrum, are the most important characters for identification, followed by the relative proportions and armature of the second and third maxillipeds, second pereopods and uropods. Most characters can be seen under a stereo-microscope without dissection but when it is necessary to examine the second maxillipeds it is usually necessary to remove one and to examine it under a magnification of at least × 50. Unfortunately not all the important characters have been described or figured for a number of species and identification is not always easy, especially in the *rubicunda*-group, where carapace markings are of little help, and sometimes where the key depends on relative lengths of appendages or their segments. In case of doubt a more complete dissection of appendages may be needed and the original descriptions consulted. Undoubtedly many species in the genus remain as yet undescribed.

KEY TO THE SPECIES OF *CAMPYLASPIS*

1	Carapace smooth, without tubercles, spines, ridges or lateral grooves	2
	Carapace with tubercles, spines or ridges, or at least a shallow groove on either side	21
2	Eyelobe small and rudimentary	3
	Eyelobe of normal size	5
3	Inner edge of merus of maxilliped 3 not serrated	***alba*** Hansen, 1920
	Inner edge of merus of maxilliped 3 serrated	4
4	Dactyl of pereopod 2 broad and little tapered	***nitens*** Bonnier, 1896
	Dactyl of pereopod 2 narrow and tapering	***nuda*** sp. nov.
5	Dorsal outline of carapace a little uneven	***pacifica*** Sars, 1887
	Dorsal outline of carapace smoothly rounded	6
6	Eye without lenses	7
	Eye with lenses visible	9
7	Maxilliped 3 with ischium, merus, carpus and propodus strongly serrated	***paeneglabra*** Stebbing, 1912
	Maxilliped 3 without conspicuous serrations	8
8	Basis of maxilliped 3 much longer than remaining segments together	***orientalis*** Calman, 1911
	Basis of maxilliped 3 shorter than the remaining segments together	***inornata*** Jones, 1969
9	Uropods at least nearly as long as the last three pleon somites together	10
	Uropods much shorter than the last three pleonites together	***guttata*** sp. nov.
10	Exopod of uropod a little longer than endopod	***pulchella*** Sars, 1871
	Exopod of uropod not longer than endopod	11
11	Dactyl of pereopod 2 at least as long as carpus and propodus together	12
	Dactyl of pereopod 2 shorter than carpus and propodus together	17
12	Dactyl of pereopod 2 longer than the carpus and propodus together	13
	Dactyl of pereopod only as long as the carpus and propodus together	15
13	Distal seta of ischiobasis of maxilliped 2 swollen distally	***mauritanica*** Bacescu & Muradian, 1972
	Distal seta of ischiobasis of maxilliped 2 normally tapered	14
14	Peduncle of the uropod twice as long as the endopod	***rubicunda*** (Lilljeborg, 1855)
	Peduncle of uropod less than twice as long as the endopod	***laevigata*** sp. nov.
15	Merus of maxilliped 3 narrow, its carpus and propodus not serrated	***angularis*** Gamô, 1960
	Merus of maxilliped 3 broad, its carpus and propodus serrated	16
16	Basis of pereopod 2 nearly half the total length of the appendage	***bonetti*** Bacescu & Muradian, 1972
	Basis of pereopod 2 little more than a third of the total length	***amblyoda*** Gamô, 1960
17	Dactyl of maxilliped 2 with two or three spines	18
	Dactyl of maxilliped 2 with four spines	19

18 Dactyl of pereopod 2 little tapered. Terminal seta of ischiobasis of maxilliped 2 slender . . . . ***glabra*** Sars, 1879
Dactyl of pereopod 2 normally tapered. Terminal seta of ischiobasis of maxilliped 2 thickened . . . . ***rufa*** Hart, 1930
19 Antennal notch deep . . . . ***kiiensis*** Gamô, 1960
Antennal notch shallow 20
20 Carpus of pereopod 1 barely longer than propodus . . . ***thompsoni*** Hale, 1945
Carpus of pereopod 1 much longer than propodus . . . ***similis*** Hale, 1945
21 Carapace with lateral furrows or ridges but without spines, tubercles or other large prominences 22
Carapace may or may not have furrows but also at least a pair of tubercles or many spines or large prominences, which may or may not form lateral ridges . . 54
22 Either side of the carapace with a faint groove which is not margined above or below by a distinct ridge or fold 23
Either side of the carapace with at least one well-formed ridge or fold . . . 31
23 Carapace with three dorso-lateral striations on either side of the mid-line ***striata*** Gamô, 1960
Carapace without dorso-lateral striations 24
24 Dactyl of pereopod 2 blunt ended and not tapering in distal half 25
Dactyl of pereopod 2 tapering to a narrower distal end 29
25 Carapace with small granules above and below the faint lateral grooves ***granulata*** Gamô, 1960
Carapace without granules 26
26 Dactyl of pereopod 2 with robust flattened terminal setae . . ***porcata*** sp. nov.
Dactyl of pereopod 2 with short terminal setae 27
27 Groove at side of carapace scarcely reaches into posterior half ***canaliculata*** Zimmer, 1936
Groove at side of carapace extends well into posterior half 28
28 Basis of maxilliped 3 much less than half as long as rest of appendage ***aulacoeis*** Le Loeuff & Intes, 1972
Basis of maxilliped 3 much more than half as long as rest of appendage ***fusiformis*** Gamô, 1960
29 Dactyl of pereopod 2 sharply tapered, with short terminal setae . ***unisulcata*** Hale, 1945
Dactyl of pereopod 2 moderately tapered, with a long end spine 30
30 Groove at side of carapace scarcely reaching into posterior half . ***tubulata*** Fage, 1945
Groove at side of carapace broadened posteriorly in female, reaching well into posterior half in male . . . . ***pumila*** Gamô, 1960
31 Carapace with four irregular, subrectangular, depressed areas on either side, bordered by prominent folds . . . . ***rupta*** Hale, 1945
Carapace not so sculptured, with carinae on either side subparallel . . . 32
32 Carapace with one oblique ridge on either side 33
Carapace with more than one ridge on either side 34
33 Peduncle of uropod very broad and only a little longer than the endopod ***platyuropus*** Calman, 1911
Peduncle of uropod slender, three times as long as endopod . . ***uniplicata*** Hale, 1945
34 Two oblique carinae arising anteriorly and extending for greater part of length of carapace on either side 35
Three or more oblique carinae extending similarly on carapace 49
35 Pseudorostrum long, at least a sixth of the total carapace length 36
Pseudorostrum shorter, less than a sixth of the total carapace length . . . 37
36 Pseudorostrum turned up at an angle to the line between its hind end and the hind end of the carapace . . . . ***vitrea*** Calman, 1906
Pseudorostrum not turned up . . . . ***pileus*** Foxon, 1932
37 Eyelobe of normal size, with lenses 38
Eyelobe small or absent, without lenses 46

38 Eyelobe linguiform, narrow and dilated distally . . . ***macrophthalma*** Sars, 1879
Eyelobe not linguiform, broad at base 39
39 Pseudorostrum turned up at a distinct angle to dorsum of carapace . ***hartae*** Lie, 1969
Pseudorostrum little or not turned up 40
40 Peduncle of the uropods not more than one-and-a-half as long as the endopod . 41
Peduncle of the uropods more than one-and-a-half as long as the endopod . . 42
41 Uropods shorter than the last three pleonites together . . ***sinuosa*** Gamô, 1960
Uropods as long as the last three pleonites together . ***jonesi*** Bacescu & Muradian, 1972
42 Dactyl of pereopod 2 shorter than the carpus . . . . ***undata*** Sars, 1865
Dactyl of pereopod 2 longer than the carpus 43
43 Dactyl of pereopod 2 not tapered and ending in a short articulated process
latidactyla Hale, 1945
Dactyl of pereopod 2 tapered, without an articulated process 44
44 Dactyl of pereopod 2 with no terminal setae . . . . . ***sulcata*** Sars, 1870
Dactyl of pereopod 2 ending in setae. 45
45 Sulcus on side of carapace undivided. . . . . . . ***minor*** Hale, 1945
Sulcus divided by a short vertical ridge . . . . . . ***legendrei*** Fage, 1951
46 Dactyl of pereopod 2 as long as the carpus and propodus together 47
Dactyl of pereopod 2 only as long as the carpus . . . . ***aperta*** Lomakina, 1958
47 Merus and propodus of maxilliped 3 unserrated . . . . ***johnstoni*** Hale, 1937
Merus and propodus of maxilliped 3 serrated 48
48 Ridges at side of carapace well separated and extending to hind end ***ovalis*** Stebbing, 1912
Ridges at side of carapace closer together and not reaching hind end . ***sticta*** sp. nov.
49 Carapace much elevated dorsally. Dactyl of pereopod 2 not tapered, without terminal spines or setae . . . . ***arcuata*** sp. nov.
Carapace not much elevated. Dactyl of pereopod 2 tapered, with terminal spines or setae 50
50 Uropod distinctly longer than the last two pleonites together, its endopod not very broad 51
Uropod not longer than the last two pleonites together, its endopod broad
crispa Lomakina, 1955
51 Lower lateral ridge on carapace branched 52
Lower lateral ridge on carapace unbranched 53
52 Upper horizontal ridge on carapace joined to ridge below by a short vertical ridge near the front . . . . ***speciosa*** Lomakina, 1955
These two ridges not joined in front by a vertical ridge . . . ***costata*** Sars, 1865
53 Dactyl of pereopod 2 as long as the carpus and propodus together ***triplicata*** Hale, 1945
Dactyl of pereopod 2 much longer than the carpus and propodus together
umbensis Gurwitsch, 1939
54 Carapace with many spines 55
Carapace with few or no spines. 59
55 Carapace with a depression on either side 56
Carapace without a depression 57
56 Lateral depression deep. Carapace with long hairs dorsally and large reticulations behind the groove . . . . ***reticulata*** Gamô, 1960
Lateral depression shallow. Carapace without hairs or reticulations ***echinata*** Hale, 1945
57 Pseudorostrum long and prominent. Only small spines present on carapace . . 58
Pseudorostrum short and strongly upturned. Some stout spines present
spinosa Calman, 1906
58 Spines confined to dorsum of carapace. Dactyl of pereopod 2 shorter than carpus
rostellata sp. nov.
Spines covering whole of carapace. Dactyl of pereopod 2 longer than carpus
aculeata sp. nov.

59 Carapace with a few low tubercles or with inconspicuous granule-like tubercles 60
Carapace with many conspicuous tubercles 76
60 Carapace with very small granule-like tubercles 61
Carapace with a few low dorsal protuberances 62
61 Ocular lobe narrow, about twice as long as wide. Dactyl of maxilliped 2 with three spines. ***laticarpa*** Hansen, 1920
Ocular lobe wider than long. Dactyl of maxilliped 2 with four spines ***roscida*** Hale, 1945
62 Carapace without distinct lateral ridges 63
Carapace with two or more lateral ridges on either side 66
63 Carapace with scattered hairs and a single pair of protuberances dorso-laterally ***pilosa*** sp. nov.
Carapace without hairs and with several dorsal protuberances 64
64 Antenna 2 of male reaching end of uropods 65
Antenna 2 of male not reaching to end of pleon ***brevicornis*** sp. nov.
65 Dactyl of maxilliped 2 with three spines. Peduncle of uropod smooth ***affinis*** Sars, 1870
Dactyl of maxilliped 2 with four spines. Peduncle of uropod serrated ***serratipes*** Hansen, 1920
66 Carapace with upper lateral ridge recurved above to form a nearly closed loop ***quadriplicata*** Lomakina, 1968
Lateral ridges on carapace not recurved 67
67 Carapace broad, with two vertical ridges on either side nearly meeting their fellows from the opposite side mid-dorsally ***bulbosa*** sp. nov.
Carapace without vertical ridges 68
68 Carapace with oblique ridges on either side defining a depressed area which is much broader behind ***redacta*** sp. nov.
Sulcus if present not much broader behind 69
69 Dorso-lateral protuberances tipped by a short spine and upper oblique ridges with a few small spines 70
Dorso-lateral protuberances and ridges without spines 71
70 Basal segment of maxilliped 2 with peculiarly thickened terminal seta ***paucispina*** sp. nov.
Terminal seta on basal segment of maxilliped 2 normally tapered. ***cognata*** sp. nov.
71 Dactyl of pereopod 2 much shorter than the carpus 72
Dactyl of pereopod 2 much longer than the carpus 73
72 Basal segment of maxilliped 2 with thickened terminal seta ***caperata*** sp. nov.
Basal segment of maxilliped 2 with terminal seta normally tapered ***plicata*** sp. nov.
73 Carapace with three horizontal ridges on either side, the upper ridge meeting its fellow dorsally towards the hind end ***valleculata*** sp. nov.
Carapace with two ridges on either side, the upper ridge not meeting its fellow on the mid-dorsal line 74
74 Pseudorostrum long and distinctly upturned ***exarata*** sp. nov.
Pseudorostrum short and not upturned 75
75 Dactyl of pereopod 2 as long as the carpus and propodus together and with three short stout terminal spines ***mansa*** sp. nov.
Dactyl of pereopod 2 longer than the carpus and propodus together and with a single short stout terminal spine and a longer seta ***bicarinata*** sp. nov.
76 Carapace with tuberculate ridges or with some of the tubercles situated in rows along the sides 77
Carapace without tuberculate ridges, nor with tubercles situated in rows along the sides 91
77 Dactyl of pereopod 2 much longer than the carpus and propodus together, and with a terminal lobe extending beyond the insertion of the most distal seta 78
Dactyl of pereopod 2 at most as long as the carpus and propodus together, and with distal setae quite terminal 79

78 Pseudorostrum relatively long and prominent. Tubercles on carapace few and large ***rostrata*** Calman, 1905

Pseudorostrum shorter and not prominent. Tubercles on carapace small and numerous ***thetidis*** Hale, 1945

79 Merus of maxilliped 3 at least one-and-a-half as long as the carpus 80

Merus of maxilliped 3 very little longer than the carpus ***maculata*** Zimmer, 1907

80 Dactyl of pereopod 2 not longer than the carpus 81

Dactyl of pereopod 2 distinctly longer than the carpus 86

81 Tuberculate ridges at sides and lower edges of carapace joined near front by a small vertical ridge, enclosing a smooth quadrilateral area ***clavata*** Lomakina, 1952

No smooth quadrilateral area at sides of carapace 82

82 Merus of maxilliped 3 very long, three times as long as the carpus ***sagamiensis*** Gamô, 1967

Merus of maxilliped 3 shorter, less than twice as long as the carpus 83

83 Sides of carapace with three folds, the two uppermost bearing large rounded tubercles ***intermedia*** Hansen, 1920

Side of carapace with two ridges, formed of conical tubercles 84

84 Uropod as long as last three pleonites together ***horrida*** Sars, 1870

Uropod only as long as last two pleonites together 85

85 Carapace with many tubercles. Merus and carpus of maxilliped 3 dentate ***papillata*** Lomakina, 1952

Carapace with comparatively few tubercles. Merus and carpus of maxilliped 3 not dentate ***paucinodosa*** sp. nov.

86 Peduncle of uropod less than one-and-a-half as long as the endopod 87

Peduncle of uropod more than one-and-a-half as long as the endopod 89

87 Merus and carpus of maxilliped 3 without teeth ***submersa*** sp. nov.

Merus and carpus of maxilliped 3 dentate 88

88 Posterior pereonites and anterior pleonites each with a pair of dorso-lateral tubercles ***squamifera*** Fage, 1929

Pereon and pleon without dorso-lateral tubercles ***torulosa*** sp. nov.

89 Pereopod 2 comparatively stout. Outer edge of merus and carpus of maxilliped 3 without teeth ***rubromaculata*** Lie, 1969

Pereopod 2 slender. Outer edge of merus and carpus of maxilliped 3 strongly dentate 90

90 Uropods longer than the last three pleonites together, the peduncle much more than twice as long as the endopod ***horridoides*** Stephensen, 1915

Uropods only as long as the last two pleonites together, the peduncle much less than twice as long as the endopod ***glebulosa*** sp. nov.

91 Merus of maxilliped 3 triangular, expanded distally and as wide as long ***frigida*** Hansen, 1908

Merus of maxilliped 3 oblong, never as wide as long 92

92 Merus of maxilliped 3 unusually slender, about three times as long as wide ***pustulosa*** Hale, 1945

Merus of maxilliped 3 not more than twice as long as wide 93

93 Merus of maxilliped 3 as long as carpus and propodus together 94

Merus of maxilliped 3 much shorter than carpus and propodus together 95

94 Tubercles on carapace low and rounded ***verrucosa*** Sars, 1865

Tubercles on carapace conical and protruding ***aspera*** Hale, 1945

95 Pleon somites without dorsal teeth, at most with feeble tubercles on the first three. 96

Pleon somites with dorsal teeth 97

96 A depressed area on either side of the carapace. Merus of maxilliped 3 triangularly expanded on inner side. Dactyl of pereopod 2 longer than carpus ***globosa*** Hansen, 1920

No depressed area on sides of carapace. Merus of maxilliped 3 not expanded on inner side. Dactyl of pereopod 2 barely as long as carpus ***nodulosa*** Sars, 1887

97 Carpus of maxilliped 3 dentate on outer side. Dactyl of pereopod 2 longer than carpus and propodus together . . . . . . ***antarctica*** Calman, 1907
Carpus of maxilliped 3 not dentate on outer side. Dactyl of pereopod 2 shorter than carpus and propodus together . . . . . . ***multinodosa*** sp. nov.

DESCRIPTIONS AND RECORDS

Genus ***CAMPYLASPIS*** G. O. Sars, 1865

Five pereon somites visible from above. Carapace strongly vaulted in the female, where it often bulges over the anterior pereon somites. Antero-lateral angles of carapace little or not at all produced. Eye unpaired and often rudimentary. Mandible with the molar process styliform. The second maxilla reduced to a simple plate without movable endites. The first maxilliped reduced with only three segments, the terminal very small. Second maxilliped with the propodus articulated at nearly a right-angle to the carpus and ending in a broad seta, the dactyl short and ending in two or more distal diverging spines. The first pereopod with the ischium not specially elongated.

Campylaspis alba Hansen, 1920

MATERIAL. 43°40·8′N, 3°35·2′W, 1739 m, 16.7.1967, 2 ♀♀; 28°06′N, 13°28′W, 1780 m, 15.3.1968, 2 ♀♀, 2 juv.

DISTRIBUTION. Previously recorded only from southwest of the Faroes, 840–918 m, and possibly from west of Ireland (Hansen, 1920), its range is now extended to the Bay of Biscay and the Canary Islands and its lower limit to 1780 m.

Campylaspis nitens Bonnier, 1896

MATERIAL. 43°35·6′N, 3°24·8W, 860 m, 15.7.1967, 2 ♀♀; 43°46·7′N, 3°38′W, 2379 m, 18.7.1967, 5 ♀♀, 3 ♂♂; 43°43′N, 3°47·8′W, 641 m, 19.7.1967, 54 ♀♀, 3 ♂♂, 14 juv.; 27°29·8′N, 15°20·1′W, 2351 m, 18.3.1968, 1 ♀; 27°14·9′N, 15°36·3′W, 2988 m, 19.3.1968, 1 ♂; 07°09′S, 34°25·5′W–07°08′S, 34°25′W, 770–805 m, 6.4.1963, 1 ♀; 7°58′S, 34°22′W, 834–939 m, 18.2.1967, 1 ♂.

DISTRIBUTION. Previously recorded from the Bay of Biscay and west of Ireland (Calman, 1905) but the latter was probably *C. alba* (see Hansen, 1920), 570–950 m. Its range is now extended to the Canary Islands and the tropical west Atlantic and its lower limit to 2988 m.

Campylaspis nuda sp. nov.
(fig. 1)

MATERIAL. 07°58′S, 34°17′W–07°50′S, 34°17′W, 943–1007 m, 20.2.1967, 4 ♀♀, 3 ♂♂; 08°03′S, 34°23′W–08°02′S, 34°25′W, 587 m, 21.2.1967, 15 ♀♀, 13 ♂♂.

DESCRIPTION. Adult female, length 3·8 mm: carapace (fig. 1a, b) smooth and vaulted, evenly rounded dorsally, projecting backwards over the first three pereonites, about one-and-a-half as long as high, more than half the total body length without

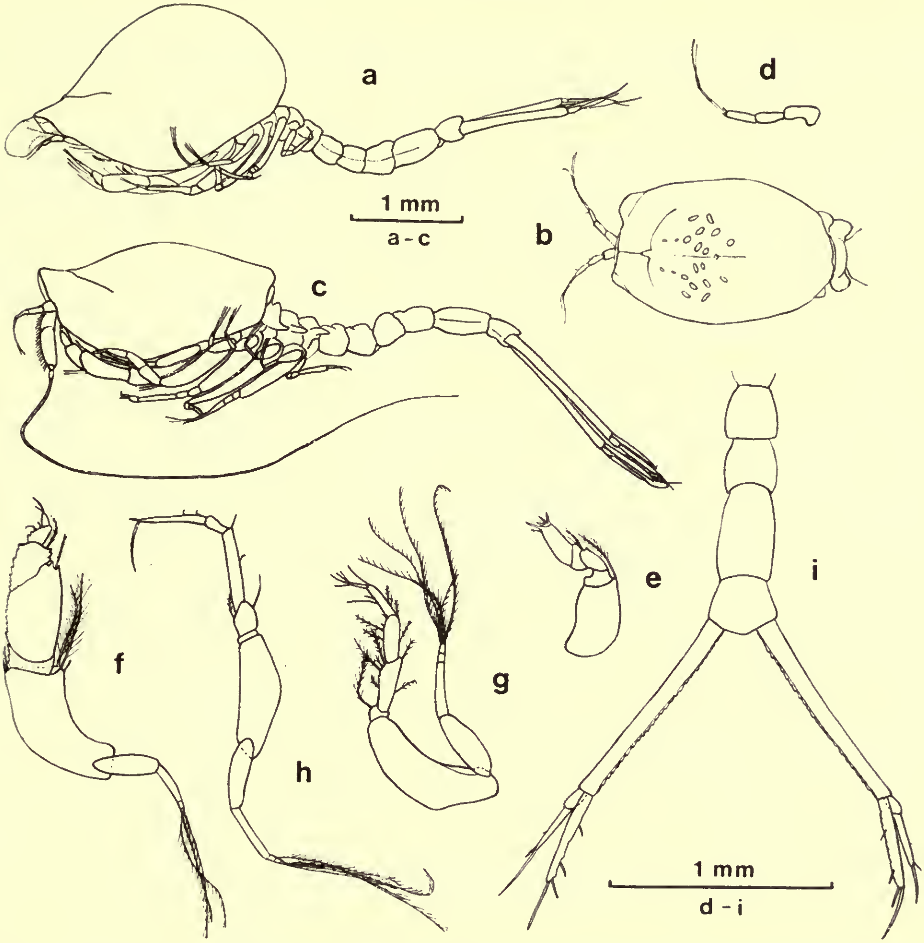

FIG. 1. *Campylaspis nuda*. a, ♀ from side ; b, ♀ carapace from above ; c, ♂ from side ; d, ♀ antenna 1 ; e, ♀ maxilliped 2 ; f, ♀ maxilliped 3 ; g, ♀ pereopod 1 ; h, ♀ pereopod 2 ; i, ♀ uropod and end of pleon.

appendages. The pseudorostrum is fairly acute, slightly downturned and less than a sixth of the total carapace length. The eyelobe is short and rudimentary.

The first antenna (fig. 1d) has the three segments of the peduncle about equal in length.

The second maxilliped (fig. 1e) has the dactyl prolonged into three nearly equal spines ; the merus with a tooth. The third maxilliped (fig. 1f) broad, the ischium, merus, carpus and propodus serrated on the inner edge, the merus and carpus also on the outer edge distally ; the basis much curved, a little shorter than the remaining segments together.

The first pereopod (fig. 1g) with the basis about as long as the remaining segments together. The second pereopod (fig. 1h) with the dactyl distinctly shorter than the carpus ; its basis is more than half as long as the remainder of the appendage.

Uropods (fig. 1i) long, about as long as the last five pleon somites together, the endopod less than half as long as the peduncle, which is serrated on its inner edge; the endopod is also somewhat serrated and has two spines on the inner edge and two unequal end spines.

Adult male, length 4·0 mm (fig. 1c): differing from the female in the usual manner, with the carapace less vaulted and less produced backwards over the pereonites. The second antenna with a long flagellum reaching beyond the end of the body. The uropods relatively longer and with more setae and spines.

Type locality. 08°03′S, 34°23′W, 587 m. Types deposited at the British Museum (Natural History). Registration numbers: Holotype 1974:283; Paratypes 1974:284.

Remarks. *C. nuda* resembles *C. nitens* and *C. alba* in having a smooth carapace with rudimentary eyelobe but differs from either of these species in the shape of the merus of maxilliped 3, which is serrated internally but broader than in *C. nitens*. The dactyl of pereopod 2 is narrower than that of *C. nitens*. All other described species of *Campylaspis* with a smooth carapace have the eyelobe well developed, although lenses have not always been distinguished, as is the case with *C. paeneglabra* Stebbing. The latter species has a much longer dactyl of pereopod 2 compared with the carpus. *C. laevigata* sp. nov. following has a reasonably well-developed eyelobe with lenses visible and the dactyl of maxilliped 2 ends in four spines instead of three. *C. guttata* sp. nov. following also has a well-developed eyelobe with lenses, while the shape and proportions of its appendages differ considerably; in particular the uropods are very much shorter.

Recorded at present off Recife, Brazil, in depths between 587 and 1007 m.

Campylaspis guttata sp. nov.

(fig. 2)

Material. 23°05′S, 12°31·5′E, 1546–1559 m, 17.5.1968, 2 ♀♀; 9°43·5′S, 10°57′E–9°29′S, 11°34′E, 2644–2754 m, 22.5.1968, 1 ♀.

Description. Adult female, length 3·7 mm: carapace (fig. 2a, b) smooth, rounded dorsally, less than one-and-a-half as long as high, antero-lateral angles rounded and not produced. Pseudorostrum blunt and less than a seventh of the total carapace length. Eyelobe well developed with lenses faintly visible. A number of small irregular reddish pigment spots are present, mainly postero-laterally but some on the frontal area.

Antenna 1 (fig. 2c) with the first segment of the peduncle stout and elbowed, a little longer than the second, which is slightly longer than the third.

Maxilliped 2 (fig. 2d) with three spines on the dactyl, the middle one short; the carpus and propodus each with a small tooth on the inner edge; the terminal seta of the ischiobasis is thickened apically. Maxilliped 3 (fig. 2e) with the basis longer than the rest of the appendage, of which none of the segments is serrated; the merus and carpus are not widened.

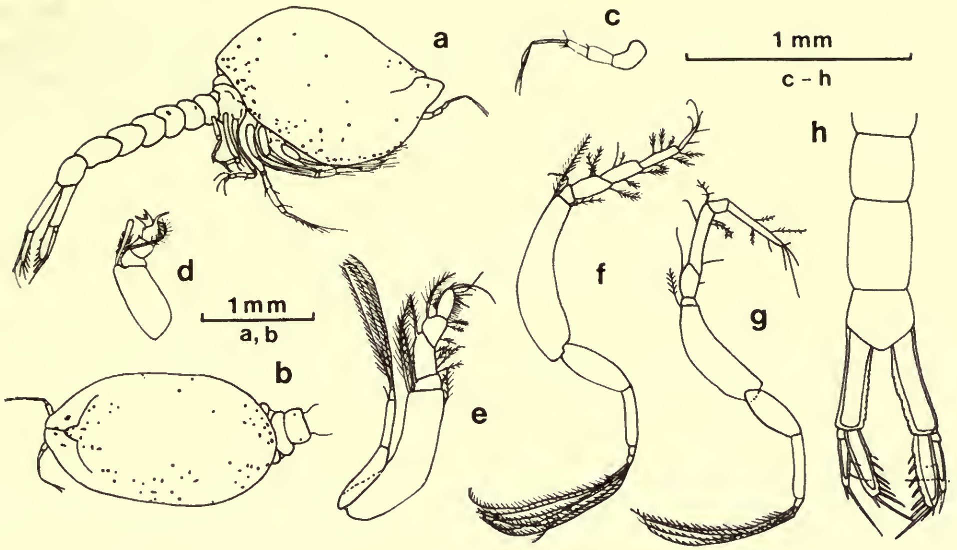

FIG. 2. *Campylaspis guttata* ♀. a, from side; b, carapace from above; c, antenna 1; d, maxilliped 2; e, maxilliped 3; f, pereopod 1; g, pereopod 2; h, uropod and end of pleon.

Pereopod 1 (fig. 2f) with the basis about as long as the rest of the appendage. Pereopod 2 (fig. 2g) with the basis more than half as long as the remaining segments together; the dactyl is about as long as the carpus.

Uropods (fig. 2h) short and broad, much shorter than the last three pleonites together, the peduncle less than one-and-a-half as long as the endopod and serrated along its inner edge; the endopod with six spines on the inner edge and two end spines, one much the longer.

TYPE LOCALITY. 23°05'S, 12°31·5'E, 1546–1559 m. Types deposited at the British Museum (Natural History). Registration numbers: Holotype 1974 : 285; Paratype 1974 : 286.

REMARKS. *C. guttata* is readily distinguished from other described species of the genus with a smooth carapace by its comparatively short uropods, which in all the others have the peduncle at least nearly as long as the last two pleonites together and in *C. guttata* is much shorter than these, and proportionately about as short as in *C. platyuropus* Calman. The latter has a ridge on either side of the carapace.

Three specimens have been collected off S.W. Africa.

Campylaspis rubicunda (Lilljeborg, 1855)

MATERIAL. 39°58·4'N, 70°40·3'W, 300 m, 28.8.1962, 1 juv.; 39°46·5'N, 70°43·3'W, 1470–1330 m, 25.8.1964, 1 ♀, 3 ♂♂; 40°1·6'N, 70°40·7'W, 196 m, 6.7.1965, 3 ♀♀, 5 ♂♂; 39°38·5'N, 70°36·5'W–39°39'N, 70°37·1'W, 2178 m, 18.12.1966, 1 ♀.

DISTRIBUTION. There have been many records from the N.E. Atlantic between Norway and the British Isles, from the Arctic, from the N.W. Atlantic between Greenland and New England and from the Okhotsk Sea in the North Pacific, at depths between 9 and 1977 m. The lower limit is now extended to 2178 m but it is essentially an inhabitant of the shelf and slope.

Campylaspis laevigata sp. nov.
(fig. 3)

MATERIAL. 47°40′N, 5°0′W, 119 m, 12.7.1967, 1 ♀, 1 ♂; 43°43′N, 3°47·8′W, 641 m, 19.7.1967, 1 ♀, 1 ♂; 46°17·5′N, 4°45·2′W, 1336 m, 24.7.1967, 3 ♀♀, 3 ♂♂; 46°16·3′N, 4°44′W, 1427 m, 25.7.1967, 1 ♀, 1 ♂; 22°54′S, 13°32′E, 205 m, 15.5.1968, 1 ♀, 3 juv.; 22°53′S, 13°31′E, 220 m, 16.5.1968, 4 ♀♀.

DESCRIPTION. Adult female, length 2·8 mm: carapace (fig. 3a, b) smooth, almost evenly rounded dorsally, a little less than twice as long as high, antero-lateral angles slightly produced. Pseudorostrum rather short, fairly acute, about a seventh of the total carapace length. Eyelobe well developed with lenses visible.

Antenna 1 (fig. 3c) with the first segment of the peduncle rather bent, distinctly longer than the second or third, which are nearly equal.

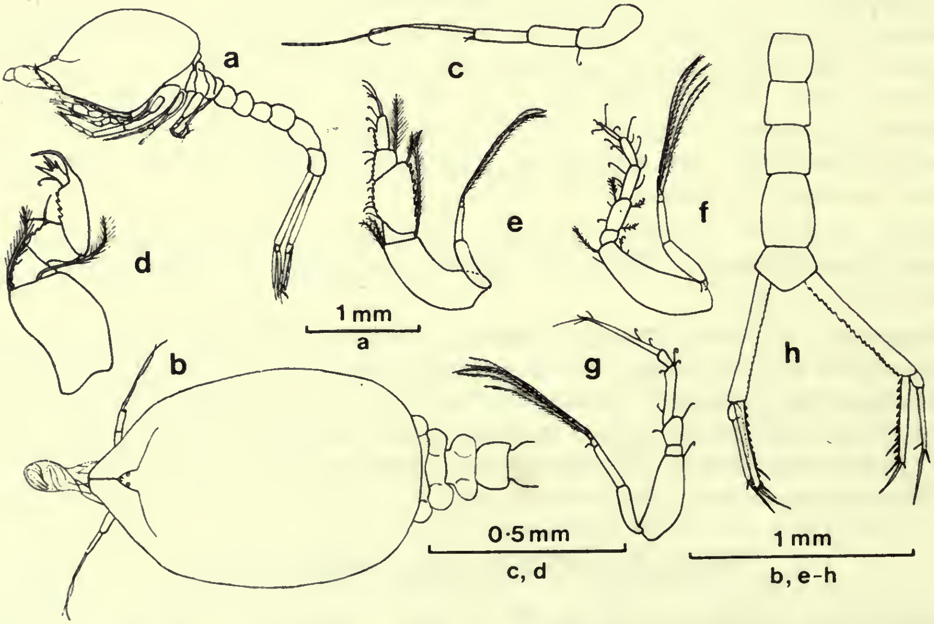

FIG. 3. *Campylaspis laevigata* ♀. a, from side; b, carapace and pereon from above; c, antenna 1; d, maxilliped 2; e, maxilliped 3; f, pereopod 1; g, pereopod 2; h, uropod and end of pleon.

Maxilliped 2 (fig. 3d) with the propodus rather long, ending in a long flattened seta; the dactyl with four spines; merus, carpus and propodus serrated along their inner edges. Maxilliped 3 (fig. 3e) with the basis distinctly shorter than the remaining segments together; the merus serrated on its outer edge and merus, carpus and propodus on the inner edge; propodus and dactyl narrow.

Pereopod 1 (fig. 3f) with the basis slightly shorter than the remaining segments together. Pereopod 2 (fig. 3g) with the basis less than half as long as rest of appendage; dactyl narrow, longer than the carpus and propodus together.

Uropods (fig. 3h) longer than the last four pleonites together, the endopod much more than half as long as the peduncle, serrated internally, with three spines on its inner edge and a long end spine.

TYPE LOCALITY. 47°40′N, 5°0′W, 119 m. Types deposited at the British Museum (Natural History). Registration numbers: Holotype 1974 : 287; Paratypes 1974 : 288.

REMARKS. *C. laevigata* resembles *C. bonetti* Bacescu & Muradian in having a smooth carapace and well-developed eyelobe with lenses and four spines on the dactyl of maxilliped 2 but the shape of the latter is rather different and the dactyl of pereopod 2 is proportionately longer. It also resembles in most respects *C. paeneglabra* Stebbing but the dactyl of maxilliped 2 in that species has only two spines according to Stebbing (1912) and its carapace has a few slight prominences. From *C. mauritanica* Bacescu & Muradian it differs in the shape of maxilliped 2 and especially that of the distal seta of the ischiobasis, which is not swollen nor tufted towards its tip. The endopod of the uropod is proportionately longer than in *C. rubicunda* Sars. The species with a smooth carapace described in Hale (1945) and Gamô (1960) all have the dactyl of pereopod 2 shorter than the carpus and propodus together.

Twenty specimens were collected in the Bay of Biscay and also off S.W. Africa between 119 and 1427 m.

Campylaspis glabra G. O. Sars, 1879

MATERIAL. 38°46′N, 70°06′W, 2886 m, 21.8.1964, 1 ♀.

DISTRIBUTION. Many specimens have been recorded from the N.E. Atlantic from Norway to Senegal in West Africa and in the Mediterranean. It has also been recorded by Fage (1945) from Vietnam but this identification, based on a single adult male, may be regarded as doubtful, as may also my own record from Senegal based on two males. The depth range was from 5 to 2827 m. The present record extends its range to the N.W. Atlantic and the lower depth range slightly to 2886 m. Like *C. rubicunda* it is an inhabitant of the shelf and slope, with a broadly overlapping but more southerly distribution.

Campylaspis porcata sp. nov.

(fig. 4)

MATERIAL. 40°37′N, 70°50′W–40°34′N, 70°51′W, 68 m, 27.11.1967, 82 ♀♀, 20 ♂♂, 3 juv.; 40°10·8′N, 70°43·6′W–40°10·6′N, 70°44′W, 123 m, 28.11.1967, 1 ♀.

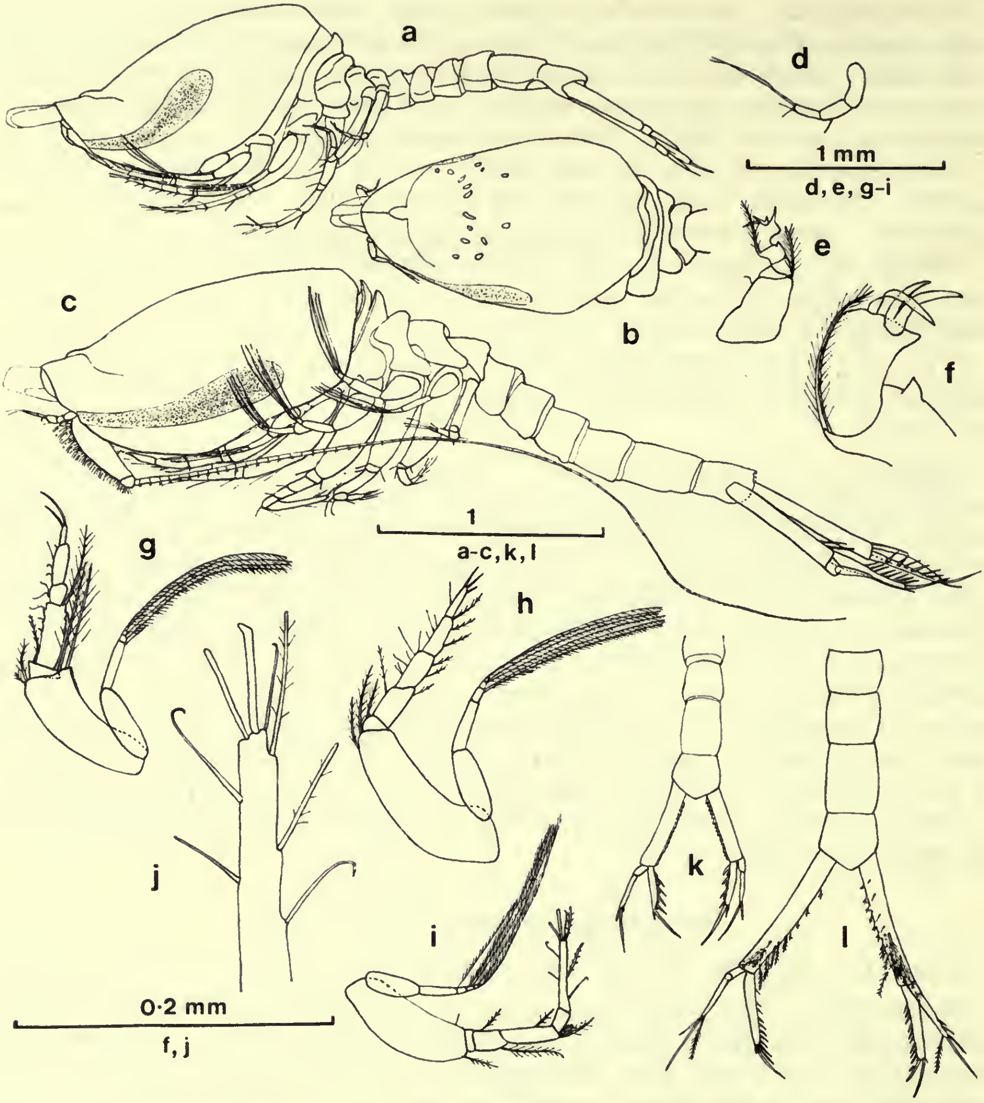

FIG. 4. *Campylaspis porcata*. a, ovigerous ♀ from side; b, ♀ from above; c, ♂ from side; d, ♀ antenna 1; e, f, ♀ maxilliped 2; g, ♀ maxilliped 3; h, ♀ pereopod 1; i, j, ♀ pereopod 2; k, ♀ uropod and end of pleon; l, ♂ uropod and end of pleon.

DESCRIPTION. Ovigerous female, length 2·3 mm: carapace (fig. 4a, b) twice as long as high, with on either side a narrow sulcus becoming a little broader towards its upper end; the dorsal surface is smooth in outline and little produced backwards. The pseudorostrum is a little less than a sixth of the total carapace length, with barely a trace of antennal notch below. The eyelobe is well developed but lenses are not visible in the preserved specimens although they seem likely to be present.

Antenna 1 (fig. 4d) with the basal segment of the peduncle about one-and-a-half as long as the distal segment.

Maxilliped 2 (fig. 4e, f) with the ischiobasis broad proximally, its apical seta slender and not very long ; the carpus and propodus each with a tooth and the dactyl with three rather long fragile spines, of which the middle is a little shorter than those on either side. Maxilliped 3 (fig. 4g) with the basis a little shorter than the rest of the appendage ; ischium with an apical tooth ; merus long and narrow and serrated on either edge.

Pereopod 1 (fig. 4h) with the basis about as long as the following segments combined. Pereopod 2 (fig. 4i) with the basis little more than two-thirds as long as the rest of the appendage ; dactyl as long as the carpus and propodus together, ending in three spines of which two are rather stout (fig. 4j).

Uropod (fig. 4k) fairly short, shorter than the last three pleonites together ; endopod more than half as long as the peduncle, which is strongly serrated along its inner edge and a little longer than the exopod ; it has four spines with some serrations interspersed along the inner edge and two unequal end spines.

Adult male, length 3·2 mm (fig. 4c, l) : differs from the female in the usual manner. The flagellum of antenna 2 reaches to the end of the uropods.

TYPE LOCALITY. 40°37′N, 70°50′W–40°34′N, 70°51′W, 68 m. Types are deposited in the British Museum (Natural History). Registration numbers : Holotype 1974 : 289 ; Paratypes 1974 : 290.

REMARKS. *C. porcata* resembles several other species in having a rather narrow sulcus on either side. These include *C. canaliculata* Zimmer, *C. unisulcata* Hale, *C. pumila* Gamô and *C. jonesi* Bacescu & Muradian but it differs from all these in the shape of the sulcus, which in none of the other species is narrow anteriorly and wider posteriorly. *C. porcata* differs from other sulcate species in the proportions of some of the appendages and especially in the armature of the dactyl of pereopod 2.

It seems possible that Calman's record of *C. affinis* (Calman, 1912), which he describes as differing from Sars' account in having on either side a shallow oblique depression and which he refers to *C. affinis* with considerable doubt, should be referred to *C. porcata.* They were found off Marthas Vineyard in 66–71 m in the same area as this species.

Many specimens were obtained off Gay Head in 68–123 m.

Campylaspis vitrea Calman, 1906

MATERIAL. 43°43′N, 3°47·8′W, 641 m, 19.7.1967, 7 ♀♀, 2 ♂♂, 16 juv.

DISTRIBUTION. Previously recorded from the Mediterranean south of Sardinia and near Capri, 950–1100 m and 1227 m, and doubtfully by Calman (1912) from the coast of Labrador in 985 m. The present record from the Bay of Biscay extends its upper depth range to 641 m and shows that it certainly occurs outside as well as within the Mediterranean.

Campylaspis macrophthalma G. O. Sars, 1879

MATERIAL. 47°40′N, 5°0′W, 119 m, 12.7.1967, 5 ♀♀.

DISTRIBUTION. Recorded from the Mediterranean between Monaco and the Straits of Messina and from Île d'Yeu in the Bay of Biscay, 38–200 m. The present record extends its range a little further to the north. This species is probably confined to the shelf.

Campylaspis sticta sp. nov.

(fig. 5)

MATERIAL. 23°0′S, 12°45′E, 1007–1014 m, 16.5.1968, 7 ♀♀.

DESCRIPTION. Adult female, length 3·3 mm: carapace (fig. 5a, b) more than twice as long as high, not at all produced over the pereon somites, with a well-defined groove on either side bounded by distinct ridges; the dorsal outline is well elevated and smooth and apart from two small protuberances on the frontal area there are no spines or other prominences. The pseudorostrum is rather upturned, less than a fifth of the total carapace length, with no trace of an antennal notch below. The eyelobe is fairly large but without lenses. The carapace, pereon and pleon, and most of the appendages have many small scattered red blotches of pigment.

Antenna 1 (fig. 5c) with the basal segment of the peduncle strongly curved, little longer than either of the more distal segments.

Maxilliped 2 (fig. 5d) with the ischiobasis long; carpus with two teeth on its inner edge; propodus ending in a slender spine and dactyl with four slender spines, of

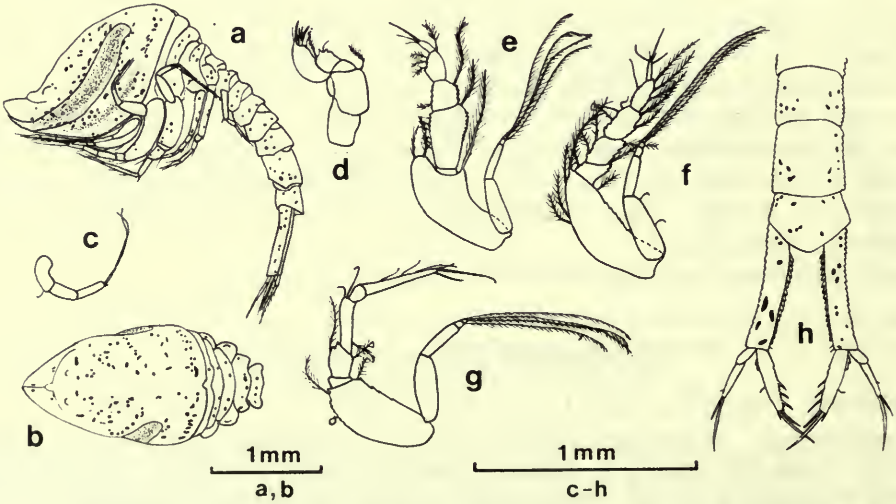

FIG. 5. *Campylaspis sticta* ♀. a, from side; b, carapace and pereon from above; c, antenna 1; d, maxilliped 2; e, maxilliped 3; f, pereopod 1; g, pereopod 2; h, uropod and end of pleon.

which the most basal is longest. Maxilliped 3 (fig. 5e) with the basis curved, as long as the ischium to propodus combined, widened at the distal end which is produced well beyond the end of the ischium ; the merus and carpus are fairly broad and serrated on both edges and the propodus on the lower edge.

Pereopod 1 (fig. 5f) with the basis almost as long as rest of appendage ; the ischium, merus, carpus and propodus are serrated on either edge. Pereopod 2 (fig. 5g) with the basis broad, a little more than half as long as the remaining segments together ; the dactyl is tapered and longer than the carpus and propodus together.

Uropod (fig. 5h) as long as the last three pleonites together, peduncle fairly broad and about twice as long as the endopod, which is distinctly longer than the exopod ; the peduncle is serrated on both edges but more distinctly on the inner edge, and the endopod has four spines and some serrations on the inner edge and two unequal end spines.

TYPE LOCALITY. 23°0'S, 12°45'E, 1007–1014 m. The types are deposited in the British Museum (Natural History). Registration numbers : Holotype 1974 : 291 ; Paratypes 1974 : 292.

REMARKS. *C. sticta* is distinguished from most species with a sulcus on either side of the carapace by the absence of lenses in the eyelobe. The sulcus differs from that of *C. porcata* in being of much the same width throughout and among other differences the dactyl of pereopod 2 is tapered and without thickened terminal spines.

Seven specimens were found off S.W. Africa in 1007–1014 m.

Campylaspis arcuata sp. nov.
(fig. 6)

MATERIAL. 8°48'S, 12°52'E, 527–542 m, 23.5.1968, 2 ♀♀.

DESCRIPTION. Adult female, length 3·3 mm : carapace (fig. 6a, b) twice as long as high, well elevated dorsally, with two long ridges on either side running back parallel with the lower edge of the carapace, joined by a vertical ridge at the hind end but not meeting the ridge from the opposite side dorsally ; a third shorter ridge is present dorsal to these, running backwards on either side from behind the side of the frontal area. The pseudorostrum is about a fifth of the total carapace length and not inclined upwards but set at a very obtuse angle to the carapace behind the eyelobe ; there is a little trace of an antennal notch below it. The eyelobe is short and without lenses.

Antenna 1 (fig. 6c) with the segments of the peduncle slender, the first strongly curved and shorter than the third.

Maxilliped 2 (fig. 6d) with the ischiobasis of moderate length, its distal seta normally pinnate ; the propodus has a distal process reaching as far as the end of the spines of the dactyl, of which there are three of about equal length. Maxilliped 3 (fig. 6e) with the basis curved, a little shorter than the rest of the appendage, the merus and carpus broadened but not serrated.

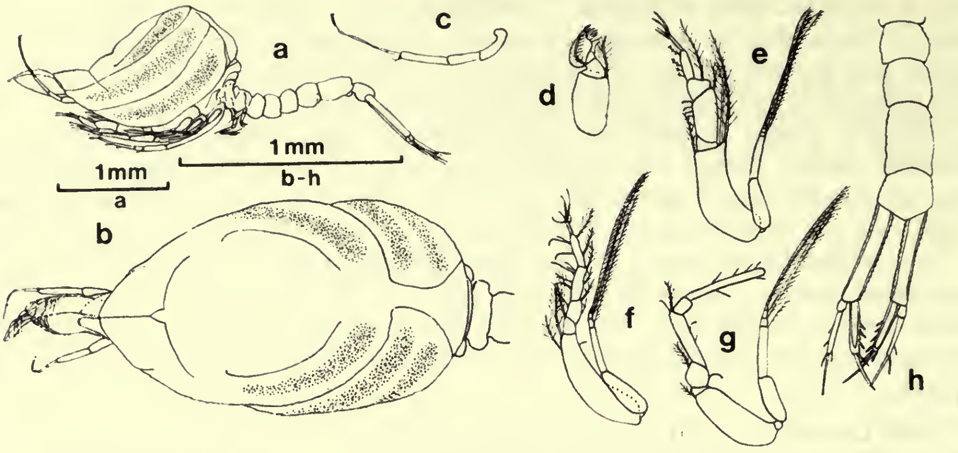

FIG. 6. *Campylaspis arcuata* ♀. a, from side; b, carapace from above; c, antenna 1; d, maxilliped 2; e, maxilliped 3; f, pereopod 1; g, pereopod 2; h, uropod and end of pleon.

Pereopod 1 (fig. 6f) with the basis very little shorter than the remaining segments together; these are without spines or serrations. Pereopod 2 (fig. 6g) with the basis less than half as long as rest of appendage; the dactyl is not tapered and without distal spines; it is about as long as the carpus and propodus together.

Uropod (fig. 6h) a little shorter than the last three pleonites combined; the peduncle is serrated on either side and twice as long as the endopod, which is only slightly longer than the exopod and has four or five spines and some serrations on its inner edge and a long end spine.

TYPE LOCALITY. 8°48′S, 12°52′E, 527–542 m. Types deposited in the British Museum (Natural History). Registration numbers: Holotype 1974 : 293; Paratype 1974 : 294.

REMARKS. *C. arcuata* resembles *C. exarata* sp. nov. a little in the shape of the carapace but it is more elevated dorsally and its pseudorostrum is not upturned, while it lacks prominences at the sides of the frontal area. The shape of the dactyl of pereopod 2 is quite different in the two species.

Two specimens were collected off S.W. Africa in 527–542 m.

Campylaspis costata G. O. Sars, 1865

MATERIAL. 39°46·5′N, 70°43·3′W, 1470–1330 m, 25.8.1964, 1 ♀.

DISTRIBUTION. Many records in the N.E. Atlantic from northern Norway to the British Isles, 23–478 m. Although apparently almost confined to the shelf in N.W. Europe this species can apparently occur on the slope off N.E. America down to about 1470 m. A subspecies, *C. c. speciosa*, has been described by Lomakina (1955) from the northern Pacific but I am inclined to regard it as a separate species.

Campylaspis spinosa Calman, 1906

Material. 28°06′N, 13°28′W, 1780 m, 15.3.1968, 2 ♀♀, 1 ♂ ; 07°09′S, 34°25·5′W–07°08′S, 34°25′W, 770–805 m, 6.4.1963, 1 juv. ; 7°58′S, 34°22′W, 834–939 m, 18.2.1967, 3 ♀♀, 1 ♂, 1 juv. ; 7°58′S, 34°17′W–7°50′S, 34°17′W, 943–1007 m, 20.2.1967, 9 ♀♀, 2 ♂♂, 1 juv. ; 8°03′S, 34°23′W–8°02′S, 34°25′W, 587 m, 21.2.1967, 56 ♀♀, 9 ♂♂, 8 juv. ; 23°0′S, 12°45′E, 1007–1014 m, 16.5.1968, 2 ♀♀.

Distribution. Recorded previously from the western Mediterranean (Calman, 1906 ; Reyss, 1972), 950–2924 m. The present records extend its geographical range to the Canaries, the tropical West Atlantic and the coast of S.W. Africa and its upper depth limit to 587 m.

Campylaspis rostellata sp. nov.
(fig. 7)

Material. 27°13′N, 15°41′W, 3301 m, 20.3.1968, 1 ♀.

Description. Adult female, length 4·2 mm : carapace (fig. 7a, b) more than twice as long as high, smooth at the sides but with fairly numerous small spines dorso-laterally and on the frontal area. The pseudorostrum is two-ninths of the total carapace length, prominent and sharply pointed when viewed from the side ; behind it the side of the carapace is produced into an antero-lateral angle, with serrations extending backwards. The eyelobe is rudimentary.

The pereon somites are serrated laterally (fig. 7b), the pleon somites laterally and the hinder ones also dorsally.

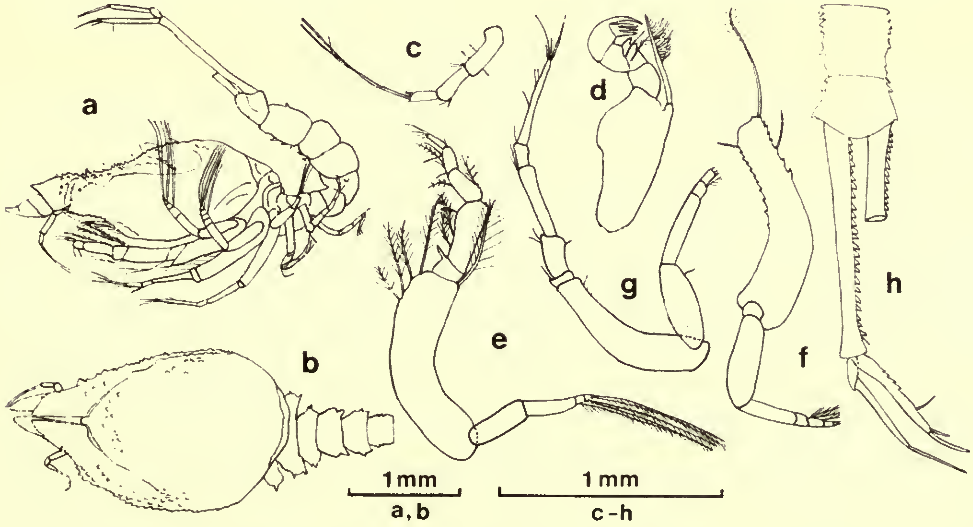

Fig. 7. *Campylaspis rostellata* ♀. a, from side ; b, carapace and pereon from above ; c, antenna 1 ; d, maxilliped 2 ; e, maxilliped 3 ; f, basis of pereopod 1 ; g, pereopod 2 ; h, uropod and end of pleon.

Antenna 1 (fig. 7c) with the basal segment of the peduncle elbowed near the base, nearly twice as long as the third segment.

Maxilliped 2 (fig. 7d) with the ischiobasis long and with a robust but not distally thickened terminal seta; carpus with two teeth on its inner edge; propodus with a long tooth and dactyl with three equal teeth. Maxilliped 3 (fig. 7e) with the basis curved, longer than rest of appendage; ischium with a tooth on the lower edge; merus nearly twice as long as the carpus, both segments with some small serrations on the upper edge.

Pereopod 1 (fig. 7f) incomplete in the specimen but the basis curved and serrated on both edges distally. Pereopod 2 (fig. 7g) with the basis about two-thirds as long as remaining segments together; merus with a terminal tooth on its lower edge; dactyl narrow and nearly as long as the carpus and propodus together.

Uropod (fig. 7h) longer than last four pleonites combined; peduncle with strong serrations along either edge, more than twice as long as the endopod, which has some serrations along the inner edge basally, two spines distally and a stout end spine; exopod about as long as the endopod, with a long slender terminal spine.

TYPE LOCALITY. 27°13′N, 15°41′W, 3301 m. Type deposited in the British Museum (Natural History). Registration number: Holotype 1974: 295.

REMARKS. *C. rostellata* somewhat resembles *C. rostrata* Calman and *C. aculeata* sp. nov. in the shape of the pseudorostrum but is easily distinguished from either by the markings of the carapace, from *C. rostrata* by the relative length of the uropods and from *C. aculeata* by its much smaller size and lack of spinulation on most of the appendages.

A single specimen was obtained off the Canary Islands in 3301 m.

Campylaspis aculeata sp. nov.

(fig. 8)

MATERIAL. 0°46′S, 29°28′W–0°46·5′S, 29°24′W, 3459 m, 14.2.1967, 3 ♀♀, 1 ♂, 4 juv.

DESCRIPTION. Ovigerous female, length 9·6 mm: carapace (fig. 8a) a little more than twice as long as high, with a mid-dorsal groove reaching from the eyelobe to near the hind end and then bifurcating obliquely; the whole surface is covered with numerous small spines. Pseudorostrum two-ninths of total carapace length, prominent and sharply pointed when viewed laterally; no antero-lateral angle is visible but the lower part of the carapace is serrated. The eyelobe is obsolete.

The first and second pereonites each have a pair of blunt mid-dorsal spines and the fourth has a ring of spines. The pleon somites have numerous spines at the sides and dorso-laterally.

Antenna 1 (fig. 8b) with the first two segments of the peduncle studded with blunt spines or serrations; the first segment nearly twice as long as the second and more than twice as long as the third.

Maxilliped 2 (fig. 8c) with the ischiobasis fairly long, the terminal pinnate seta long and slender; there are five spines on the inner edge of the carpus; the propodus

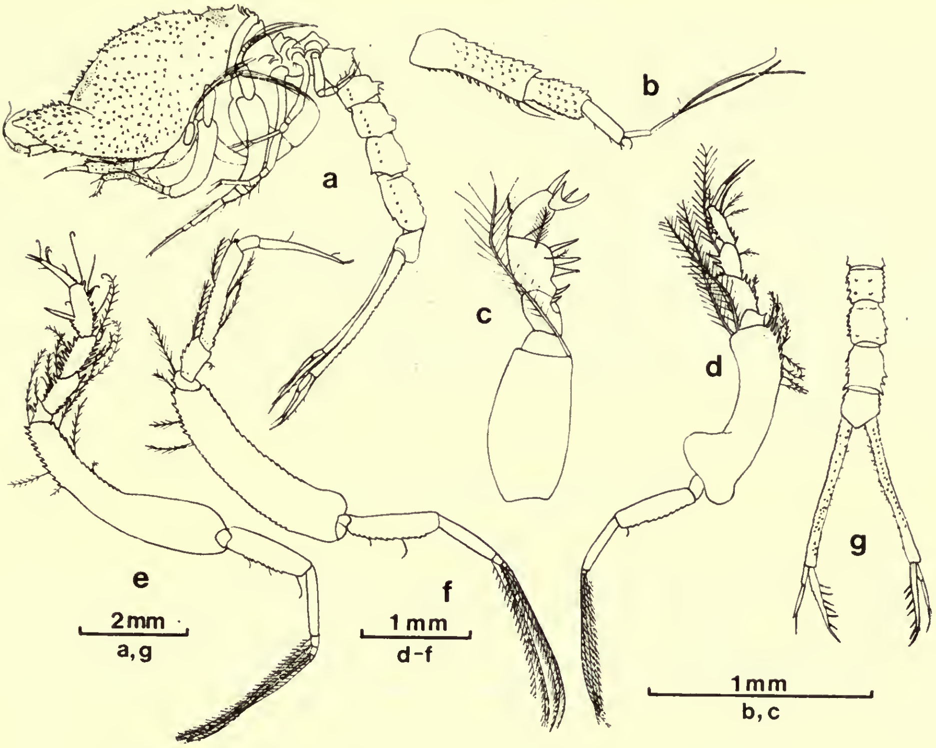

FIG. 8. *Campylaspis aculeata* ovigerous ♀. a, from side ; b, antenna 1 ; c, maxilliped 2 ; d, maxilliped 3 ; e, pereopod 1 ; f, pereopod 2 ; g, uropod and end of pleon.

has one terminal spine and the dactyl three of nearly equal length. Maxilliped 3 (fig. 8d) with the basis curved, broadened basally, a little longer than the remaining segments together, with a number of spines on the lower edge ; ischium, merus, carpus and propodus all have one or a number of spines on one or both edges.

Pereopod 1 (fig. 8e) with the basis curved, distinctly longer than the other segments combined ; all the segments have a number of spines or serrations, the merus, carpus and propodus on both edges, and the propodus also has a long spine on the lower edge. Pereopod 2 (fig. 8f) with the basis a little shorter than the rest of the appendage, serrated on both edges, as is the carpus along its basal part ; the propodus is much shorter than the carpus.

Uropod (fig. 8g) longer than the last five pleonites together ; the peduncle is nearly two-and-a-half as long as the endopod, which is distinctly longer than the exopod ; the peduncle has many short spines and serrations and the endopod has six slender spines on its inner edge and a longer end spine.

TYPE LOCALITY. 0°46′S, 29°28′W–0°46·5′S, 29°24′W, 3459 m. The types are deposited in the British Museum (Natural History). Registration numbers : Holotype 1974 : 296 ; Paratypes 1974 : 297.

REMARKS. *C. aculeata* is unusually large for the genus. The shape of the carapace is rather similar to that of *C. rostellata* sp. nov. but it is much more spiny. The spines are much smaller than in *C. spinosa* Calman and the pseudorostrum is not upturned as in that species. From *C. echinata* Hale it is distinguished by the shape of the carapace and of the second maxillipeds and second pereopods, among other details.

In general shape and size this species approaches the genus *Campylaspides* Fage, and especially to *Campylaspides spinifera* Jones (1973). However, although the shape of its second maxillipeds might be thought to represent a transitional stage towards *Campylaspides*, having several well-developed carpal spines, the propodus and dactyl retain the form typical of *Campylaspis*.

Eight specimens were found near the mid-Atlantic Ridge between Dakar and Recife in 3459 m.

Campylaspis brevicornis sp. nov.

(fig. 9)

MATERIAL. 23°02'S, 12°19'E, 2117–2154 m, 17.5.1968, 1 ♂.

DESCRIPTION. Adult male, length 3·8 mm: carapace (fig. 9a, b) more than twice as long as high, with some small rounded prominences dorsally and with numerous short hairs, the dorsal outline not much elevated and rather irregular.

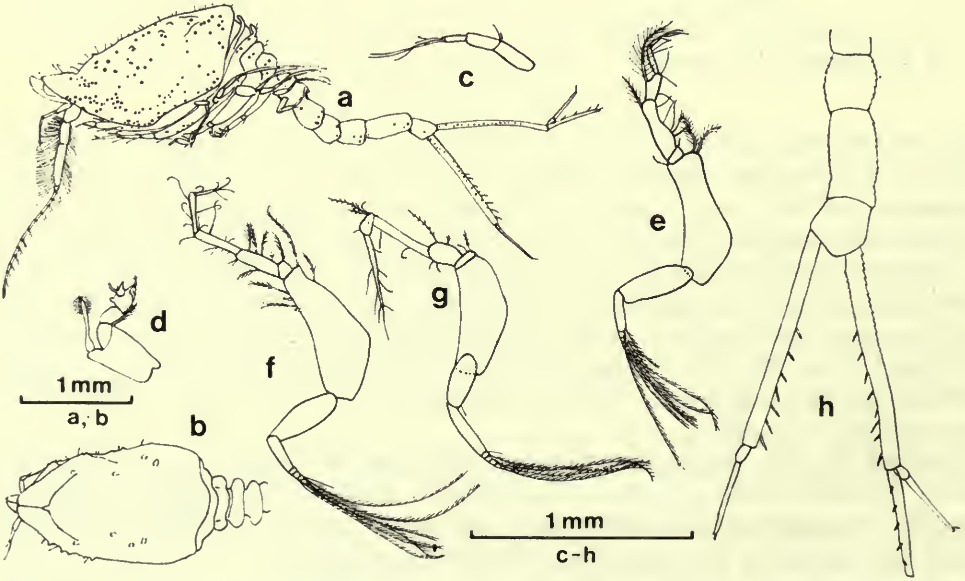

FIG. 9. *Campylaspis brevicornis* ♂. a, from side; b, carapace and pereon from above; c, antenna 1; d, maxilliped 2; e, maxilliped 3; f, pereopod 1; g, pereopod 2; h, uropod and end of pleon.

Pseudorostrum fairly large and prominent ; antero-lateral angle not at all produced and some infero-lateral serrations present. Eyelobe rudimentary.

The first two pereonites with dorsal projections. The whole body and most of the appendages have numerous small reddish pigment spots.

Antenna 1 (fig. 9c) with the segments of the peduncle decreasing successively in length, the basal segment straight and nearly twice as long as the third. Antenna 2 (fig. 9a) with the flagellum rather short, not reaching beyond the pereon.

Maxilliped 2 (fig. 9d) with the ischiobasis broad, its distal seta thickened and with a distal tuft of hairs ; the propodus with a fairly short distal seta and a small tooth on its inner edge ; the dactyl with three spines, the middle one small. Maxilliped 3 (fig. 9e) with its segments fairly narrow, unarmed, the basis as long as the remaining segments together, with two rather short and thick pinnate setae distally ; the merus long and narrowed distally, more than twice as long as the carpus.

Pereopod 1 (fig. 9f) with the basis broadened proximally, a little shorter than the rest of the appendage. Pereopod 2 (fig. 9g) with the basis a little more than half as long as the rest of the appendage ; the dactyl narrowed distally, about as long as the carpus.

Uropod (fig. 9h) incomplete in the specimen but longer than the pleon, the peduncle about twice as long as the endopod ; the peduncle has about eight spines on its inner edge and the endopod at least five.

TYPE LOCALITY. 23°02'S, 12°19'E, 2117–2154 m. Type deposited in the British Museum (Natural History). Registration number : Holotype 1974 : 298.

REMARKS. It is difficult to see if the flagellum of the second antenna is complete but it is certainly shorter than usual for the genus and distinguishes the adult male from other species with a similarly prominent pseudorostrum.

A single male was found off S.W. Africa in 2117–2154 m.

Campylaspis pilosa sp. nov.
(fig. 10)

MATERIAL. 7°08'S, 34°17'W–7°50'S, 34°17'W, 943–1007 m, 20.2.1967, 5 ♀♀, 1 ♂ ; 8°03'S, 34°23'W–8°02'S, 34°25'W, 587 m, 21.2.1967, 5 ♀♀.

DESCRIPTION. Adult female, length 4·0 mm : carapace (fig. 10a, b) about twice as long as high, with a blunt prominence on either side of the frontal area and an ill-defined groove on either side above and below it ; a number of moderately long hairs are scattered over the dorsal surface. The pseudorostrum is more than a sixth of the total carapace length and the antero-lateral angle is slightly produced on either side below it. The eyelobe is rudimentary.

Some blunt spines and numerous short hairs are present on the sides of the pleon somites.

Antenna 1 (fig. 10c) with the peduncle segments slender, the first a little curved.

Maxilliped 2 (fig. 10d) with the ischiobasis broad, its distal seta much thickened at the distal end ; propodus with a fairly stout spine distally and a prominent tooth on

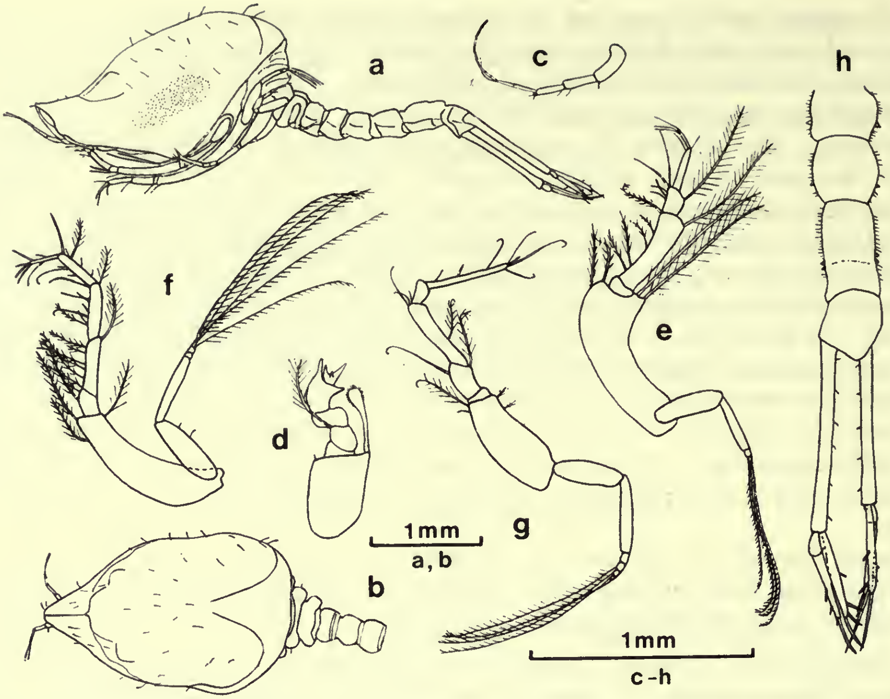

FIG. 10. *Campylaspis pilosa* ♀. a, from side; b, carapace and pereon from above; c, antenna 1; d, maxilliped 2; e, maxilliped 3; f, pereopod 1; g, pereopod 2; h, uropod and end of pleon.

the inner side; dactyl with three spines, the middle one small. Maxilliped 3 (fig. 10e) with the basis a little shorter than the remaining segments together and strongly curved, the other segments slender and unarmed, the merus nearly twice as long as the propodus.

Pereopod 1 (fig. 10f) fairly slender, with the basis much shorter than the rest of the appendage. Pereopod 2 (fig. 10g) with the basis about half as long as remaining segments together; the dactyl narrow, about as long as the carpus.

Uropod (fig. 10h) about as long as the last four pleonites together, the endopod a little less than half as long as the peduncle, which has a few setae along its inner edge; the endopod has three spines and one terminal spine and is about as long as the exopod, which has several short spines along its outer edge and a long end spine.

TYPE LOCALITY. 8°03′S, 34°23′W–8°02′S, 34°25′W, 587 m. Types deposited in the British Museum (Natural History). Registration numbers: Holotype 1974 : 299; Paratypes 1974 : 300.

REMARKS. The rather hairy carapace without any other projections except the two antero-lateral prominences distinguish this species from others with a lateral groove.

Twelve specimens have been collected off Recife, Brazil, in 587–1007 m.

Campylaspis bulbosa sp. nov.
(fig. 11)

Material. 23°02'S, 12°19'E, 2117–2154 m, 17.5.1968, 5 ♀♀.

Description. Immature female, length 3·3 mm : carapace (fig. 11a, b) less than twice as long as high, broad and bulbous, with a well-defined ridge on either side running from below the pseudorostrum backwards to the dorsal side about three-quarters of the carapace length from the front, where it is joined by a short transverse ridge with some blunt teeth to its fellow on the opposite side ; near the lower edge of the carapace is a less prominent ridge ; two further short transverse ridges are present on either side of the frontal area, not quite meeting on the mid-line, the more anterior with a low prominence in the middle on either side ; below the long ridge is a large oval shallow depression and a further small depression is present on either side dorsally behind the posterior transverse ridge ; there are a few scattered hairs on the dorsal surface. The pseudorostrum is short, only about an eighth of the total carapace length and there is little trace of an antennal notch. The eyelobe is small but broad, without lenses.

Antenna 1 (fig. 11c) with the basal segment of the peduncle curved, more than one-and-a-half as long as the distal segment.

Maxilliped 2 (fig. 11d) with the ischiobasis broad, its distal seta rather short but not thickened ; the propodus has a tooth on its inner edge and a long distal spine

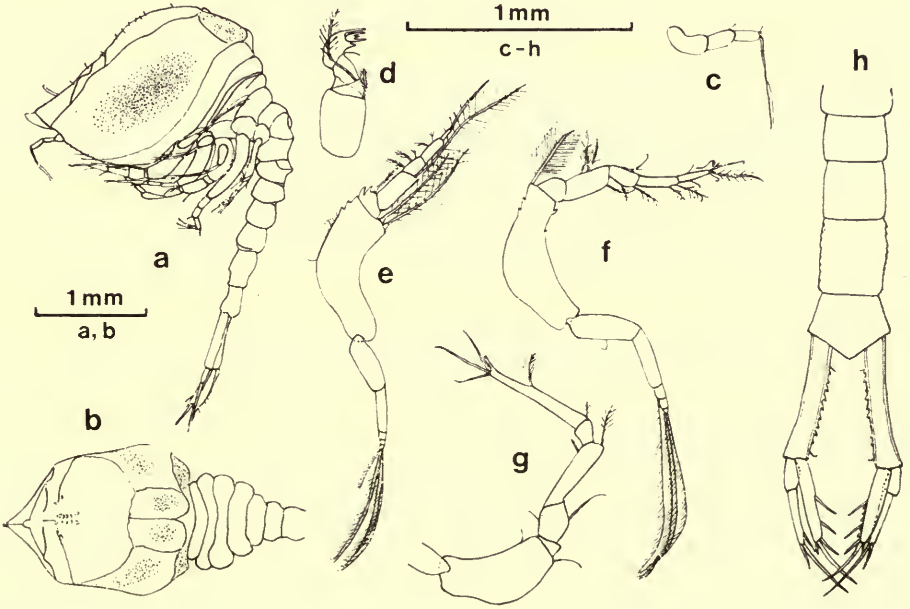

Fig. 11. *Campylaspis bulbosa* immature ♀. a, from side ; b, carapace and pereon from above ; c, antenna 1 ; d, maxilliped 2 ; e, maxilliped 3 ; f, pereopod 1 ; g, pereopod 2 ; h, uropod and end of pleon.

and the dactyl has three spines of which the middle is fairly short. Maxilliped 3 (fig. 11e) with the basis strongly curved, longer than the remaining segments together; the ischium has two sharp teeth on the lower edge and the merus is fairly narrow, with a distal tooth on the upper edge.

Pereopod 1 (fig. 11f) with the basis curved, as long as the following four segments together. Pereopod 2 (fig. 11g) with the basis a little less than a third of the total length; the dactyl is broad basally, a little longer than the carpus and propodus together, and has three long slender terminal spines and a single thicker short blunt spine.

Uropod (fig. 11h) with the peduncle about as long as the last three pleonites combined and serrated along its inner edge; the endopod is two-thirds as long as the peduncle and very slightly shorter than the exopod; it has three slender spines and a few serrations along the inner edge and two unequal end spines.

TYPE LOCALITY. 23°02′S, 12°19′E, 2117–2154 m. Types deposited in the British Museum (Natural History). Registration numbers: Holotype 1974 : 301; Paratypes 1974 : 302.

REMARKS. *C. bulbosa* is distinguished by the shape and markings of the carapace from any other known species in the genus.

Five females, none of them fully grown, occurred off S.W. Africa in 2117–2154 m.

Campylaspis redacta sp. nov.

(fig. 12)

MATERIAL. 8°03′S, 34°23′W–8°02′S, 34°25′W, 587 m, 21.2.1967, 15 ♀♀, 8 ♂♂.

DESCRIPTION. Immature male, length 2·2 mm: carapace (fig. 12a, b) less than twice as long as high, with a large irregular sulcus on either side not bounded by raised carinae and with some hollows and irregularities dorsally. The pseudorostrum is slightly downturned, a little less than a fifth of the total carapace length, and there is no antennal notch. The eyelobe is rudimentary and minute.

The fourth and fifth pereonites have a number of dorsal teeth.

Antenna 1 (fig. 12c) has the third segment of the peduncle almost as long as the basal segment.

Maxilliped 2 (fig. 12d) with the ischiobasis long, its distal seta slender; the propodus is long, with a very long spine, and the dactyl has three equal spines. Maxilliped 3 (fig. 12e) with the basis short and broad, much shorter than the remaining segments together; the merus is long, more than twice as long as the propodus, while the carpus is very short.

Pereopod 1 (fig. 12f) with the basis distinctly shorter than the rest of the appendage. Pereopod 2 (fig. 12g) with the basis not much more than half as long as the rest of the appendage; the dactyl is fairly slender and longer than the carpus and propodus together.

Uropod (fig. 12b) slightly longer than the last three pleonites together; the exopod is nearly as long as the endopod, which is more than half as long as the peduncle; the peduncle is serrated along its inner edge and has a number of short setae while the endopod has five spines on the inner edge and a long end spine.

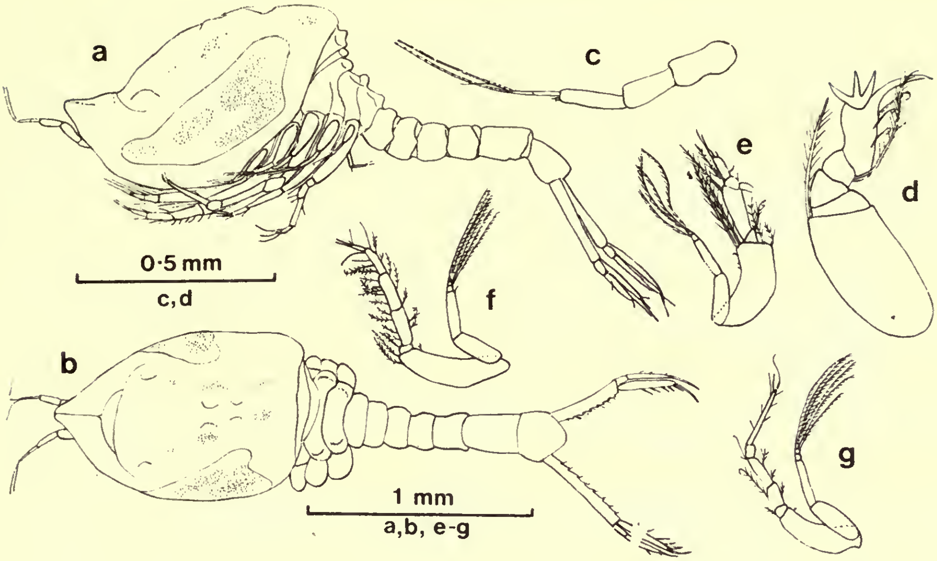

FIG. 12. *Campylaspis redacta* subadult ♂. a, from side ; b, from above ; c, antenna 1 ; d, maxilliped 2 ; e, maxilliped 3 ; f, pereopod 1 ; g, pereopod 2.

TYPE LOCALITY. 8°03′S, 34°23′W–8°02′S, 34°25′W, 587 m. Types deposited in the British Museum (Natural History). Registration numbers : Holotype 1974 : 303 ; Paratypes 1974 : 304.

REMARKS. The length of the largest specimen was 3·0 mm but none was mature. In having a fairly large sulcus on either side of the carapace *C. redacta* somewhat resembles *C. cognata* sp. nov. but there are many differences in the appendages. In *C. sulcata* Sars the sulcus is of a different shape and the latter species has a well-developed eyelobe with lenses.

Twenty-three specimens were collected off Recife, Brazil, in 587 m.

Campylaspis paucispina sp. nov.
(fig. 13)

MATERIAL. 39°26′N, 70°33′W, 2496 m, 21.8.1964, 2 ♀♀ ; 39°46·5′N, 70°43·3′W, 1470–1330 m, 25.8.1964, 17 ♀♀, 2 ♂♂ ; 39°48·7′N, 70°40·8′W, 1102 m, 6.7.1965, 7 ♀♀ ; 39°43·6′N, 70°37·4′W, 2022 m, 4.5.1966, 8 ♀♀.

DESCRIPTION. Adult female, length 4·2 mm : carapace (fig. 13a) twice as long as high, integument rather scabrous, not much elevated, with two ill-defined oblique ridges on either side with a slight hollow between them, somewhat undulating with a few smallish spines on them at intervals ; there are some more spines or slight prominences on the dorsal surface. The pseudorostrum is less than a fifth of the total carapace length and is slightly upturned ; the antero-lateral angle is slightly

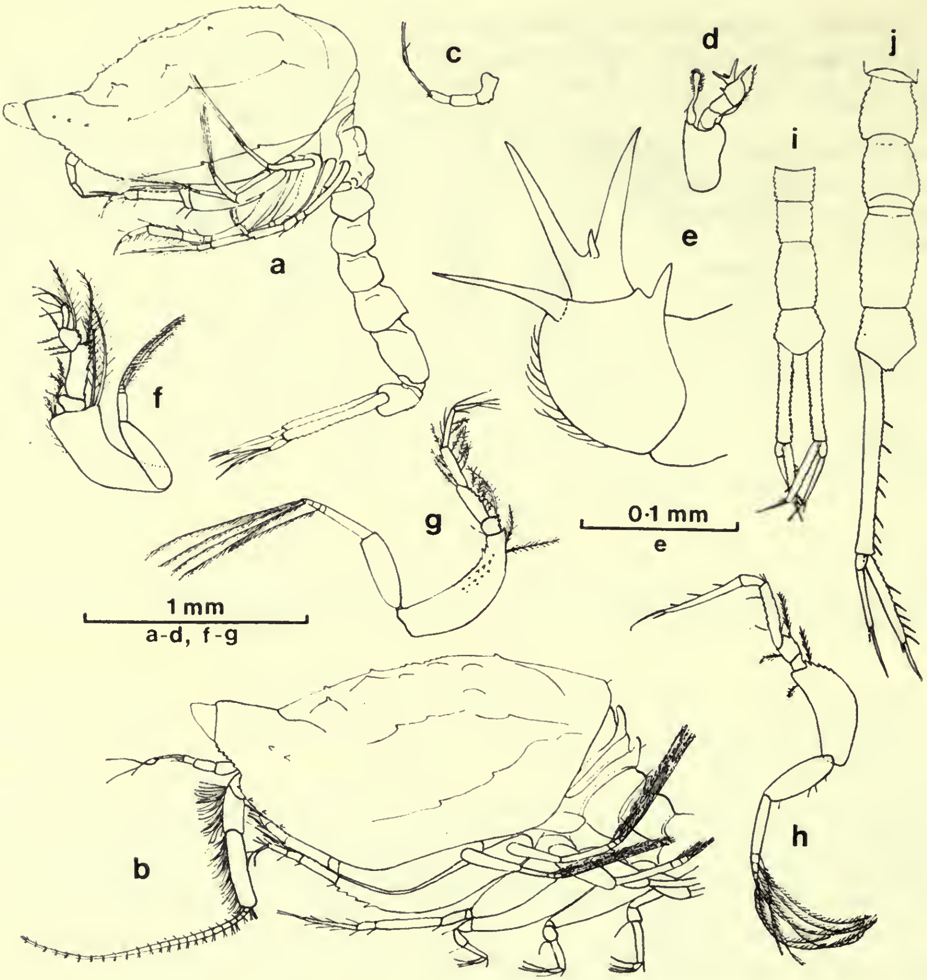

FIG. 13. *Campylaspis paucispina.* a, ♀ from side ; b, ♂ carapace and pereon from side ; c, ♀ antenna 1 ; d, e, ♀ maxilliped 2 ; f, ♀ maxilliped 3 ; g, ♀ pereopod 1 ; h, ♀ pereopod 2 ; i, ♀ uropod and end of pleon ; j, ♂ uropod and end of pleon.

produced and the infero-lateral edge is serrated behind it. The eyelobe is rudimentary.

Antenna 1 (fig. 13c) with the segments of the peduncle differing little in length, the basal segment curved and serrated below.

Maxilliped 2 (fig. 13d, e) has the apical seta on the ischiobasis thickened, with a distal brush of hairs ; the propodus has a longish distal spine and a shorter spine on its inner edge ; the dactyl has three spines of which the middle is very small. Maxilliped 3 (fig. 13f) with the basis curved, a little shorter than the remaining segments together ; the merus is long and the carpus broad, both segments serrated along the upper edge.

Pereopod 1 (fig. 13g) with the basis curved, shorter than the rest of the appendage, with some spines on its outer side ; the ischium is serrated below and the carpus above. Pereopod 2 (fig. 13h) with the basis about half as long as the remainder of the appendage ; the dactyl is as long as the carpus and propodus combined ; the carpus is serrated on its upper edge.

Uropod (fig. 13i) nearly as long as the last four pleonites together, the peduncle about one-and-a-half as long as the endopod, which is a little longer than the exopod ; the peduncle is strongly serrated on either edge and the endopod has a few spines on the inner edge and a longer end spine.

Adult male, length 3·8 mm : differs from the female in the usual manner. The first two pereonites are produced dorsally. The second antennal flagellum is long (fig. 13b, j).

TYPE LOCALITY. 39°26'N, 70°33'W, 2496 m, 21.8.1964. Types deposited in the British Museum (Natural History). Registration numbers : Holotype 1974 : 305 ; Paratypes 1974 : 306.

REMARKS. In having a carapace with comparatively few protuberances and rather ill-defined lateral ridges this species resembles *C. intermedia* Hansen but in the latter the prominences are mostly larger and blunter and the antero-lateral angle is more developed. The shape of the distal seta of the ischiobasis of maxilliped 2 resembles that of *C. affinis* Sars and also of some of the other species described here but none of these has a similarly marked carapace.

A fair number of specimens were collected south of Gay Head between 1102 and 2496 m.

Campylaspis cognata sp. nov.

(fig. 14)

MATERIAL. 8°02'S, 34°03'W–7°56'S, 34°09'W, 1493 m, 19.2.1967, 1 ♀ ; 7°58'S, 34°17'W–7°50'S, 34°17'W, 943–1007 m, 20.2.1967, 20 ♀♀, 6 ♂♂ ; 8°03'S, 34°23'W–8°02'S, 34°25'W, 587 m, 21.2.1967, 10 ♀♀, 12 ♂♂.

DESCRIPTION. Ovigerous female, length 2·7 mm : carapace (fig. 14a, b) more than twice as long as high with a sulcus of moderate breadth on either side defined by low keels, the uppermost of which has two blunt spines ; dorsal outline fairly smooth but a fairly large prominence bearing a spine is present on either side below the frontal area. The pseudorostrum is less than a fifth of the total carapace length and there is a slightly excavated antennal notch below it. The eyelobe is fairly well developed, though without lenses. Twelve embryos were contained in the brood pouch.

The first three pereonites are broad (fig. 14b) and the first three pleonites have some dorso-lateral spines.

Antenna 1 (fig. 14d) with the basal segment of the peduncle curved, distinctly longer than the third segment.

Maxilliped 2 (fig. 14e) with the ischiobasis broad, its terminal feathered seta slender ; propodus with an end spine of moderate length and a prominent tooth on the inner edge ; dactyl with three spines, the middle one small. Maxilliped 3

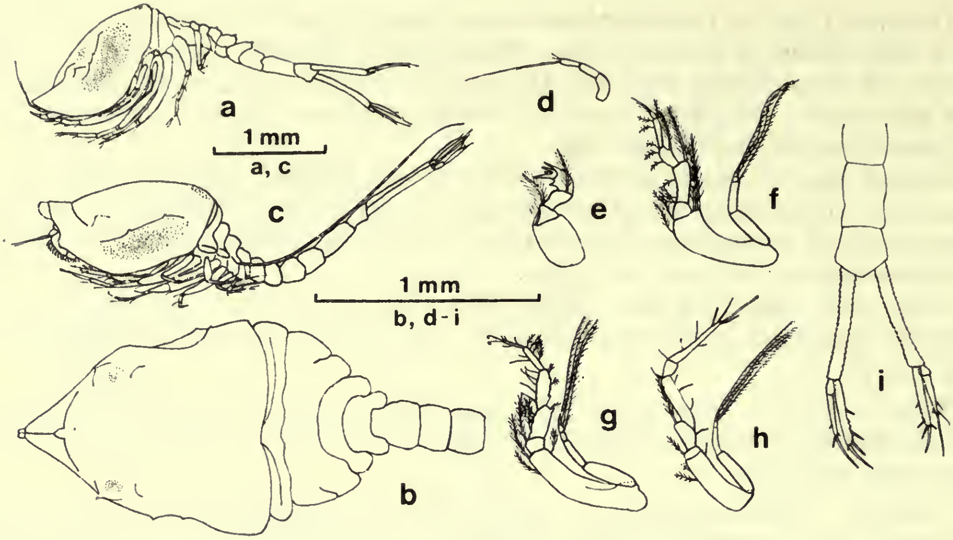

FIG. 14. *Campylaspis cognata*. a, ♀ from side; b, ♀ carapace and pereon from above; c, ♂ from side; d, ♀ antenna 1; e, ♀ maxilliped 2; f, ♀ maxilliped 3; g, ♀ pereopod 1; h, ♀ pereopod 2; i, ♀ uropod and end of pleon.

(fig. 14f) with the basis broadened distally, only a little shorter than the remaining segments combined; the merus is about twice as long as the carpus and not very much longer than the propodus.

Pereopod 1 (fig. 14g) with the basis very slightly shorter than the rest of the appendage; the merus has a tooth distally and the carpus several serrations along the upper edge. Pereopod 2 (fig. 14h) with the basis less than half as long as the remaining segments together; the dactyl is fairly broad proximally and has a long robust distal spine; it is slightly shorter than the carpus and propodus together.

Uropod (fig. 14i) longer than the last three pleonites together, the peduncle serrated along both edges; the endopod is rather more than half as long as the peduncle and distinctly longer than the exopod, with some serrations and three spines along the inner edge and two unequal end spines.

Adult male, length 3·0 mm (fig. 14c): differs from the female in the usual characters. The antennal notch is deeper and the pseudorostrum more truncated. The second antennal flagellum reaches to the end of the uropods.

TYPE LOCALITY. 8°03′S, 34°23′W–8°02′S, 34°25′W, 587 m. Types deposited in the British Museum (Natural History). Registration numbers: Holotype 1974: 307; Paratypes 1974: 308.

REMARKS. The size of the eyelobe and the shape and proportions of maxillipeds 2 and 3 and pereopod 2 among other characters differentiate this species from *C. redacta*. The presence of a few blunt spines distinguish it from other sulcate species.

A fairly large number of specimens were obtained off Recife, Brazil, between 587 and 1493 m.

Campylaspis caperata sp. nov.
(fig. 15)

MATERIAL. 10°30′N, 17°51·5′W, 1624–1796 m, 5.2.1967, 5 ♀♀, 6 ♂♂.

DESCRIPTION. Adult female, length 3·8 mm: carapace (fig. 15a, b) much less than twice as long as high, covered with minute spiny scales and with a few hairs, with two oblique ridges on either side, the lower one less well defined, and two more short transverse ridges behind the frontal area; there are a number of undulations and prominences, especially dorsally. The pseudorostrum is less than a sixth of the total carapace length, truncated, with a shallow antennal notch below. The eyelobe is rudimentary.

Antenna 1 (fig. 15c) with the segments of the peduncle fairly slender, the first distinctly less than twice as long as the third.

Maxilliped 2 (fig. 15d) with the ischiobasis broad, its terminal seta thickened and tufted apically; propodus with a long terminal spine and dactyl with three spines of which the middle is very small. Maxilliped 3 (fig. 15e) with the basis curved, broadened distally, much shorter than the remaining segments combined; the merus is about twice as long as the carpus and both are unarmed.

Pereopod 1 (fig. 15f) with the basis nearly as long as the remainder of the appendage, all the segments of which are unserrated. Pereopod 2 (fig. 15g) with the basis about two-thirds as long as the remaining segments together; the propodus is very

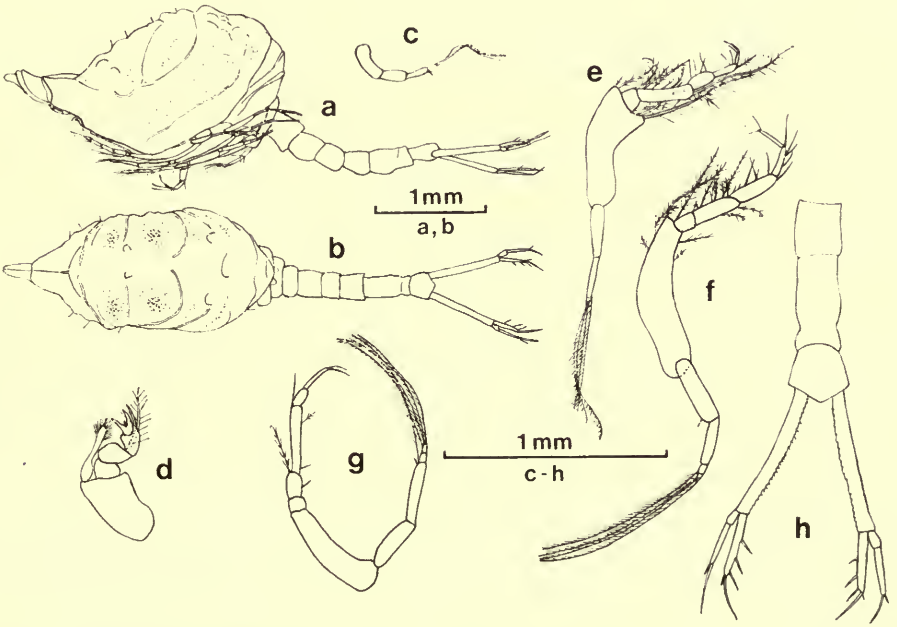

FIG. 15. *Campylaspis caperata* ♀. a, from side; b, from above; c, antenna 1; d, maxilliped 2; e, maxilliped 3; f, pereopod 1; g, pereopod 2; h, uropod and end of pleon.

short, only a third as long as the carpus, while the dactyl is a little less than half as long as the carpus.

Uropod (fig. 15h) a little longer than the last three pleonites together ; the endopod is less than half as long as the peduncle, which is serrated along its inner edge ; the endopod has three slender spines on its inner edge and one longer and a shorter end spine ; the exopod is almost as long as the endopod.

TYPE LOCALITY. 10°30′N, 17°51·5′W, 1624–1796 m. Types deposited in the British Museum (Natural History). Registration numbers : Holotype 1974 : 309 ; Paratypes 1974 : 310.

REMARKS. The combination of ridges and irregular prominences on the carapace is unlike that of any other species. *C. caperata* is also distinguished by the shortness of the dactyl of pereopod 2 compared with other species.

Eleven specimens were collected off Dakar in 1624–1796 m.

Campylaspis plicata sp. nov.

(fig. 16)

MATERIAL. 7°58′S, 34°17′W–7°50′S, 34°17′W, 943–1007 m, 20.2.1967, 4 ♀♀, 6 ♂♂.

DESCRIPTION. Adult female, length 4·8 mm : carapace (fig. 16a, b) about twice as long as high, with two oblique ridges on either side, the anterior ridge bifurcating behind the side of the frontal area to cross the dorsal surface and join with its fellow from the other side ; on the dorsal surface there are a number of low spines, with a larger prominence on either side of the frontal area. The pseudorostrum is less than a fifth of the total carapace length and fairly sharply pointed when viewed laterally, with a shallow antennal notch below, followed by some serrations. The eyelobe is rudimentary.

The first two pereonites are raised dorsally.

Antenna 1 (fig. 16d) with the basal segment of the peduncle about twice as long as the third.

Maxilliped 2 (fig. 16e) with the ischiobasis fairly long ; the merus has one tooth and the carpus two ; the propodus ends in a long slender spine and the dactyl has three fairly long spines of almost equal length. Maxilliped 3 (fig. 16f) with the basis curved, broadened distally and serrated along the distal lower edge ; the merus is a little broadened distally and serrated, and the carpus is fairly broad ; carpus and propodus have serrations along the lower edge.

Pereopod 1 (fig. 16g) with the basis about two-fifths as long as the rest of the appendage, serrated on either edge distally ; the ischium has a single tooth on the lower edge and the merus, carpus and propodus are serrated on either edge. Pereopod 2 (fig. 16h) with the basis three-quarters as long as the rest of the appendage ; the dactyl is narrow, about two-thirds as long as the carpus, and ends in a thick spine.

Uropod (fig. 16i) about as long as the last four pleonites together, the peduncle serrated on either edge ; the endopod is much longer than the exopod and more than half as long as the peduncle, with three spines on its serrated inner edge and a longer end spine.

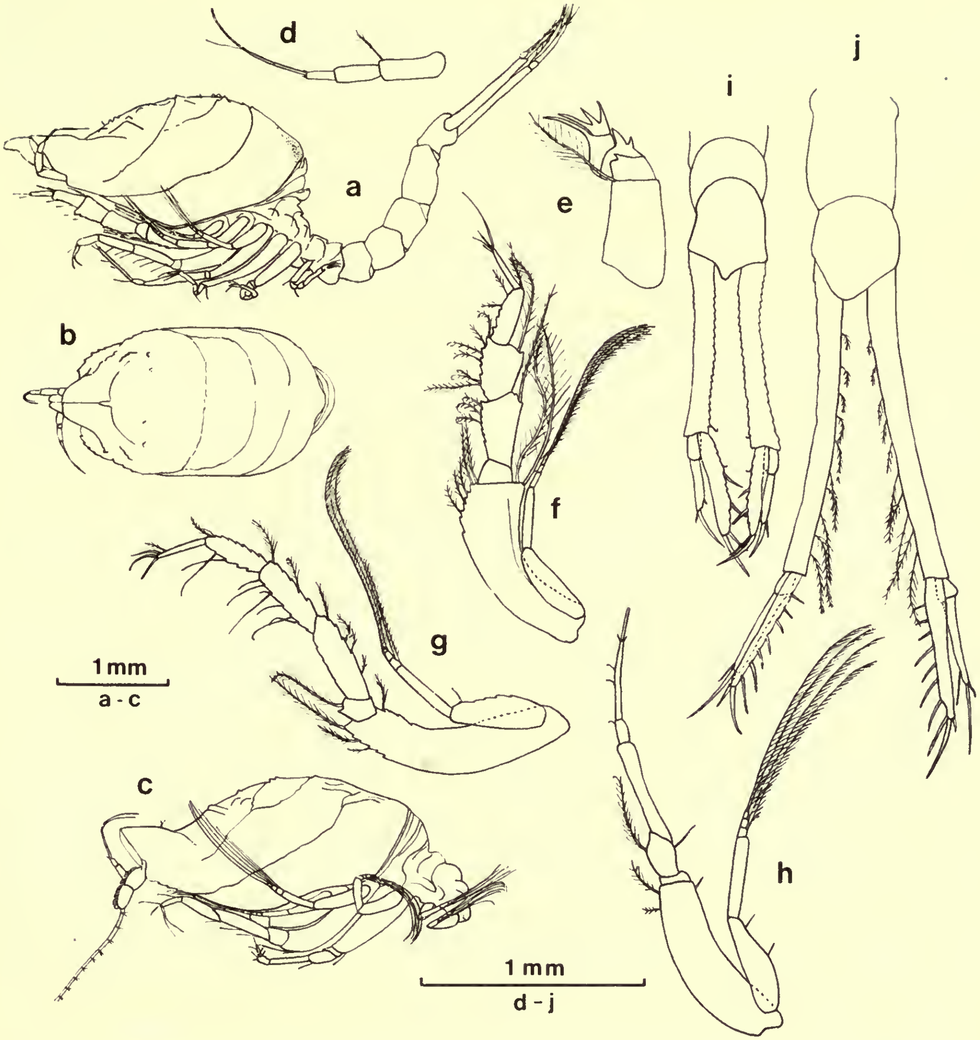

Fig. 16. *Campylaspis plicata.* a, ♀ from side; b, ♀ from above; c, ♂ carapace and pereon from side; d, ♀ antenna 1; e, ♀ maxilliped 2; f, ♀ maxilliped 3; g, ♀ pereopod 1; h, ♀ pereopod 2; i, ♀ uropod and end of pleon; j, ♂ uropod and end of pleon.

Adult male, length 5·3 mm (fig. 16c, j): differs from the female in the usual manner. The second antennal flagellum reaches to the end of the uropods which are proportionately longer than in the female and have a number of feathered setae along the inner edge and about eight spines on the inner edge of the endopod.

Type locality. 7°58′S, 34°17′W–7°50′S, 34°17′W, 943–1007 m. Types deposited in the British Museum (Natural History). Registration numbers: Holotype 1974 : 311; Paratypes 1974 : 312.

Remarks. In general appearance *C. plicata* somewhat resembles *C. caperata* but differs in the relative shapes and proportions of the appendages, among which may be mentioned the terminal seta of the ischiobasis of maxilliped 2, which is not thickened as it is in *C. caperata*, while the latter species lacks serrations on maxilliped 3 and pereopod 1.

Ten specimens were found off Recife, Brazil, in 943–1007 m.

Campylaspis valleculata sp. nov.

(fig. 17)

Material. 38°46′N, 70°06′W, 2886 m, 21.8.1964, 29 ♀♀, 18 ♂♂, 38 juv.; 38°46·7′N, 70°08·8′W, 2802 m, 21.8.1964, 5 ♀♀, 2 ♂♂; 38°16′N, 71°47′W, 2864 m, 24.8.1964, 4 ♀♀, 1 juv.; 39°38·3′N, 67°57·8′W, 2862 m, 29.6.1965, 1 ♀, 1 juv.; 39°48·7′N, 70°40·8′W, 1102 m, 6.7.1965, 1 ♀, 2 juv.; 39°37′W, 66°47′W–39°37·5′N, 66°44′W, 3806 m, 24.8.1966, 2 ♀♀.

Description. Adult female, length 6·7 mm: carapace (fig. 17a, b) more than twice as long as high, with three well-defined ridges on either side, the upper minutely crenulated and running backwards from below the front of the pseudorostrum to meet its fellow from the other side on the mid-line, where it curves forward at rather less than a sixth of the total carapace length from the hind end; the middle ridge runs backwards nearly parallel to the uppermost from well below and behind the antero-lateral angle, with a slight upward curve near the hind end of the carapace after which it dips to join its fellow from the other side to define the hind end; an undulating ridge joins the middle ridge from the top of the upward curve obliquely forward to the upper ridge; the lower ridge starts a little below the middle one and runs backwards parallel with the lower edge of the carapace to end below the upward curve of the middle ridge; there are several blunt prominences on either side of the frontal area and a number of scattered short hairs dorsally. The pseudorostrum is a little less than a sixth of the total carapace length and fairly acute from the side; there is only a faint indication of an antennal notch and antero-lateral angle. The eyelobe is fairly long and narrow, without lenses.

Antenna 1 (fig. 17d) with the segments of the peduncle long and narrow, the basal strongly curved and nearly twice as long as the third.

Maxilliped 2 (fig. 17e) with the ischiobasis moderately long, its distal seta fairly short; the propodus has a small tooth on the inner edge and a long end process; the dactyl has three spines, the middle one very small. Maxilliped 3 (fig. 17f) with the basis only a little shorter than the rest of the appendage; all the segments are comparatively slender.

Pereopod 1 (fig. 17g) with the basis curved, about as long as the remaining segments together. Pereopod 2 (fig. 17h) with the basis more than half as long as rest of appendage; the dactyl is tapered, its terminal spines not thickened, and is distinctly longer than the carpus and propodus together.

Uropod (fig. 17i) about as long as the last four pleonites together, the peduncle faintly serrated and with a few short setae along the inner edge; it is nearly three

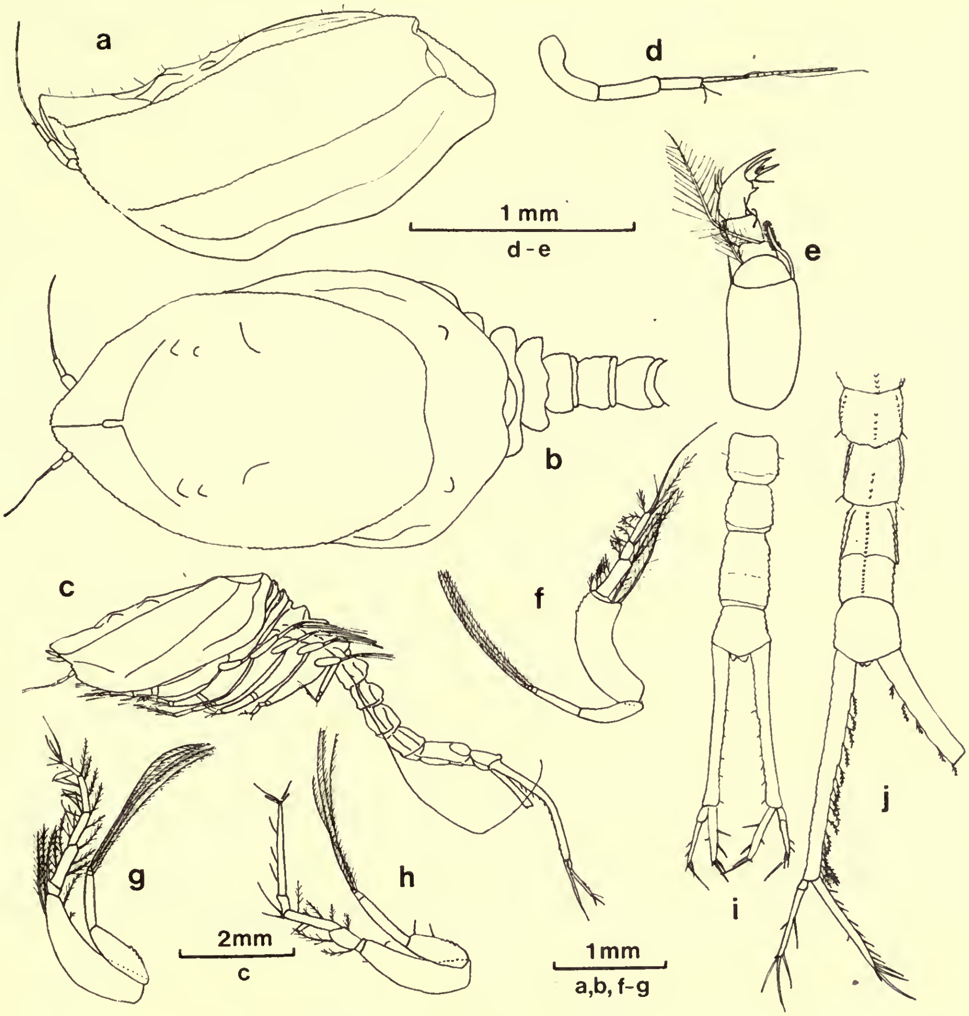

FIG. 17. *Campylaspis valleculata.* a, ♀ carapace from side ; b, ♀ carapace and pereon from above ; c, ♂ from side ; d, ♀ antenna 1 ; e, ♀ maxilliped 2 ; f, ♀ maxilliped 3 ; g, ♀ pereopod 1 ; h, ♀ pereopod 2 ; i, ♀ uropod and end of pleon ; j, ♂ uropod and end of pleon.

times as long as the endopod, which has three slender spines on the inner edge and two unequal end spines ; the exopod is only a little shorter than the endopod.

Adult male, length 8·1 mm (fig. 17c, j) : differs from female in the usual characters ; the second antennal flagellum reaches to the end of the uropods.

TYPE LOCALITY. 38°46′N, 70°06′W, 2886 m. Types deposited in the British Museum (Natural History). Registration numbers : Holotype 1974 : 313 ; Paratypes 1974 : 314.

REMARKS. *C. valleculata* is large for the genus. The shape of the carapace is somewhat similar to that of *C. undata* Sars and *C. mansa* sp. nov. but it is distinguished from either by the presence of a third lower ridge on either side and by a number of other characters.

Many specimens were obtained on the Gay Head – Bermuda transect between 1102 and 3806 m.

Campylaspis exarata sp. nov.
(fig. 18)

MATERIAL. 8°03′S, 34°23′W–8°02′S, 34°25′W, 587 m, 21.2.1967, 6 ♀♀.

DESCRIPTION. Adult female, length 4·7 mm : carapace (fig. 18a, b) about two-and-a-half as long as high, produced backwards to overhang the anterior pereonites, with two well-defined, somewhat undulating ridges running obliquely backwards, more or less parallel with the lower edge of the carapace ; the upper edge does not reach as far as the mid-dorsal line ; a fairly large blunt prominence is present on either side of the frontal area. The pseudorostrum is more than a fifth of the total

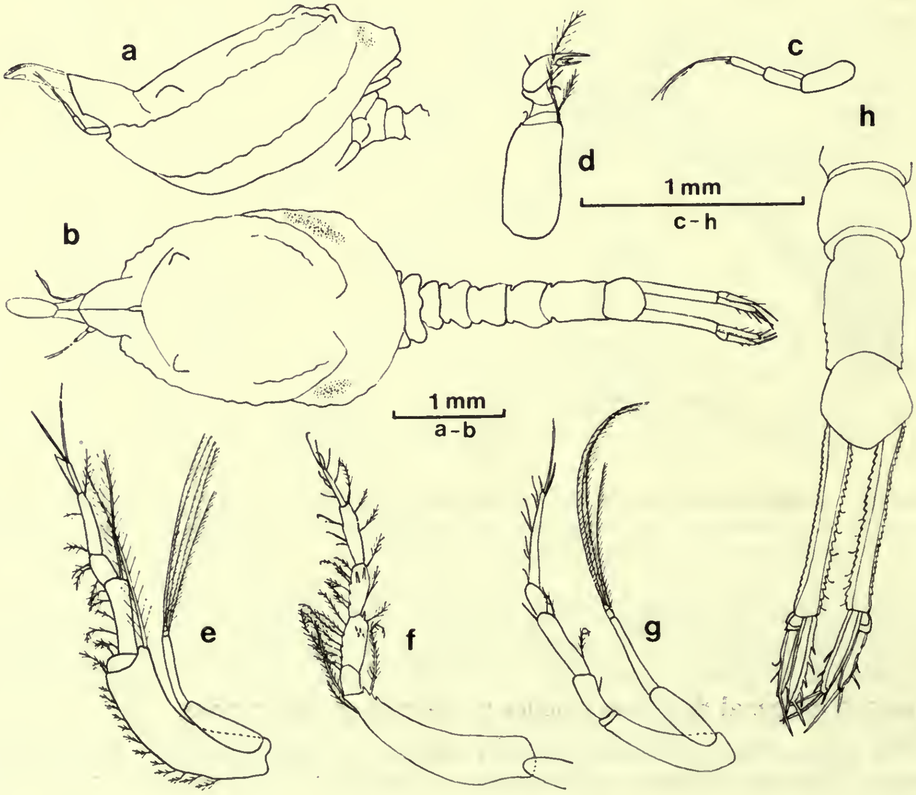

FIG. 18. *Campylaspis exarata* ♀. a, carapace from side ; b, from above ; c, antenna 1 ; d, maxilliped 2 ; e, maxilliped 3 ; f, pereopod 1 ; g, pereopod 2 ; h, uropod and end of pleon.

carapace length and is obliquely upturned, with a distinctly excavated antennal notch below. The eyelobe is small and narrow, without lenses.

Antenna 1 (fig. 18c) with the basal segment of the peduncle straight, about one-and-a-half as long as the third segment.

Maxilliped 2 (fig. 18d) with the ischiobasis fairly long, its distal seta slender and normally pinnate ; propodus with a fairly slender terminal process reaching well beyond the dactyl, which has three spines, the middle small. Maxilliped 3 (fig. 18e) with the basis curved, distinctly shorter than the rest of the appendage, and with the upper distal part somewhat produced ; the remaining segments are rather slender and unserrated.

Pereopod 1 (fig. 18f) with the basis a little shorter than remaining segments combined, somewhat curved, with several teeth on the distal upper edge ; the merus and carpus are serrated on the lower edge and have a number of spines on the outer side. Pereopod 2 (fig. 18g) with the basis narrow, little more than half as long as the rest of the appendage ; the dactyl is tapered, with several slender spines distally, and is shorter than the carpus and propodus combined.

Uropod (fig. 18h) about as long as the last three pleonites together ; the peduncles are strongly serrated on either side and about twice as long as the endopod, which is a little longer than the exopod and has four spines on its inner edge and two unequal end spines.

TYPE LOCALITY. 8°03′S, 34°23′W–8°02′S, 34°25′W, 587 m. Types deposited in the British Museum (Natural History). Registration numbers : Holotype 1974 : 315 ; Paratypes 1974 : 316.

REMARKS. *C. exarata*, with its lateral ridges on the carapace and upturned pseudorostrum, considerably resembles *C. vitrea* Calman. However, the rear dorsal side of the carapace has a different appearance, the uppermost ridge being in *C. vitrea* joined by its fellow from the opposite side by a short ridge passing straight across the top of the carapace. Among other differences the dactyl of pereopod 2 in *C. vitrea* is distinctly longer than the carpus and propodus combined.

Six specimens were collected off Recife, Brazil, in 587 m.

Campylaspis mansa sp. nov.

(fig. 19)

MATERIAL. 38°46′N, 70°06′W, 2886 m, 21.8.1964, 2 ♀♀, 3 ♂♂ ; 32°10·5′N, 64°40·7′W, 2291 m, 6.8.1966, 4 ♀♀ ; 32°19.4′N, 64°34·9′W–32°19′N, 64°34·8′W, 1135–1153 m, 18.8.1966, 97 ♀♀, 19 ♂♂, 10 juv. ; 32°15·8′N, 64°31·6′W–31°16·1′N, 64°32·6′W, 2095–2223 m, 19.8.1966, 13 ♀♀, 5 ♂♂, 8 juv.

DESCRIPTION. Immature male, length 3·5 mm : carapace (fig. 19a, b) a little more than twice as long as high, not much elevated, with two rather irregular but well-defined ridges on either side running backwards more or less parallel with the lower posterior edge ; the lower ridge extends back as far as the hind dorsal edge of the carapace ; there are a few blunt prominences dorsally and a larger rotundity on either side of the frontal area. The pseudorostrum is about a seventh of the total

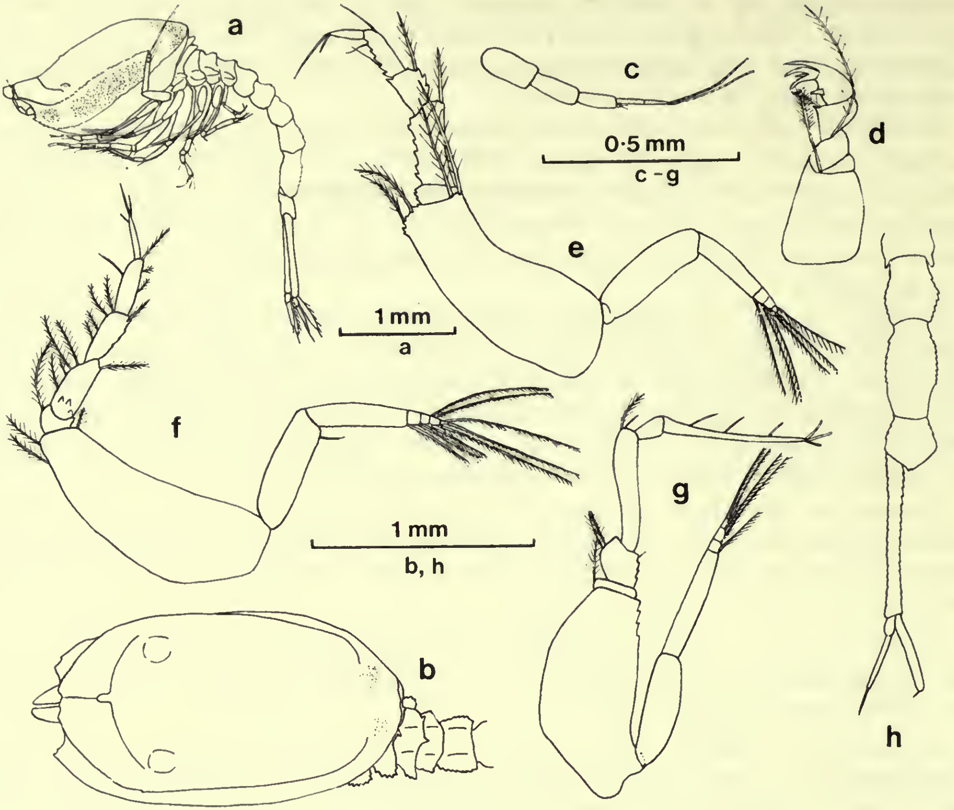

FIG. 19. *Campylaspis mansa* subadult ♂. a, from side; b, carapace and pereon from above; d, maxilliped 2; e, maxilliped 3; f, pereopod 1; g, pereopod 2; h, uropod and end of pleon.

carapace length, with a well-excavated antennal notch below, bounded by an antero-lateral tooth, with some obtuse serrations behind. The eyelobe is rudimentary, fairly narrow.

The pereon and pleon somites have some dorsal teeth and lateral serrations. The anterior pereonites have dorsal elevations.

Antenna 1 (fig. 19c) with the basal segment of the peduncle straight, about one-and-a-half as long as the third segment.

Maxilliped 2 (fig. 19d) with the ischiobasis broad, its terminal seta slender and normally pinnate; there is a tooth on the inner edge of the carpus and of the propodus, which has a long end spine; the dactyl has three spines, the middle rather small. Maxilliped 3 (fig. 19e) with the basis broad basally, about as long as the rest of the appendage; the merus is narrow and serrated on the lower edge; the carpus has serrations on the upper edge and one terminal tooth on the lower edge while the propodus is serrated along the lower edge.

Pereopod 1 (fig. 19f) with the basis a little longer than remaining segments together; the carpus is serrated along the upper edge. Pereopod 2 (fig. 19g) with the basis more than half as long as the rest of the appendage, rather broad; the merus is serrated on the upper edge; the dactyl is slender and tapering, as long as the carpus and propodus together, with three stout spines distally.

Uropod (fig. 19h) distinctly longer than the last three pleonites together, the peduncle slender, serrated on both edges and more than twice as long as the endopod; the exopod is about as long as the endopod.

Adult male, length 5·0 mm: differs from the immature male in the usual characters. The flagellum of antenna 2 is as long as the body with the uropods.

TYPE LOCALITY. 38°46′N, 70°06′W, 2886 m. Types deposited in the British Museum (Natural History). Registration numbers: Holotype 1974 : 317; Paratypes 1974 : 318.

REMARKS. *C. mansa* somewhat resembles *C. undata* Sars in the presence of two well-defined ridges on either side of the carapace. *C. undata*, however, has a large eyelobe with lenses and the dactyl of pereopod 2 is of quite a different shape.

Numerous specimens occurred on the Gay Head – Bermuda transect between 1135 and 2886 m.

Campylaspis bicarinata sp. nov.
(fig. 20)

MATERIAL. 36°23′N, 67°58′W, 4680 m, 23.8.1964, 2 ♂♂; 37°59·2′N, 79°26·2′W; 3834 m, 5.7.1965, 6 ♀♀, 2 ♂♂; 0°03′S, 27°48′W, 3730–3783 m, 13.2.1967, 1 ♀, 0°46′S, 29°28′W–0°46·5′S, 29°24′W, 3459 m, 14.2.1967, 18 ♀♀, 11 ♂♂; 7°58′S, 34°22′W, 834–939 m, 18.2.1967, 3 ♂♂; 7°58′S, 34°17′W–7°50′S, 34°17′W, 943–1007 m, 20.2.1967, 2 ♀♀, 1 ♂, 1 juv.

DESCRIPTION. Adult female, length 4·2 mm: carapace (fig. 20a, b) about twice as long as high, not greatly elevated dorsally, with two well-defined ridges on either side running backwards more or less parallel with the lower edge, the lower ridge defining the hind dorsal edge of the carapace and the upper ridge ending short of the mid-line; there is a small spine on the mid-dorsal line behind the eyelobe but no other prominences. The pseudorostrum is not upturned, less than a fifth of the total carapace length, with an obtuse antero-lateral angle below it and some serrations behind. The eyelobe is not very large, without lenses.

The anterior pereonites are elevated dorsally.

Antenna 1 (fig. 20d) with the segments of the peduncle fairly slender, the first moderately curved, about one-and-a-half as long as the third.

Maxilliped 2 (fig. 20e) with the ischiobasis long, its terminal seta fairly short but not much thickened; there is a tooth on the inner edge of the carpus and of the propodus, of which the terminal process reaches beyond the spines of the dactyl; there are three of these, the middle one very small. Maxilliped 3 (fig. 20f) with the basis curved, longer than the rest of the appendage; the remaining segments are fairly slender, the merus and carpus serrated on the upper edge.

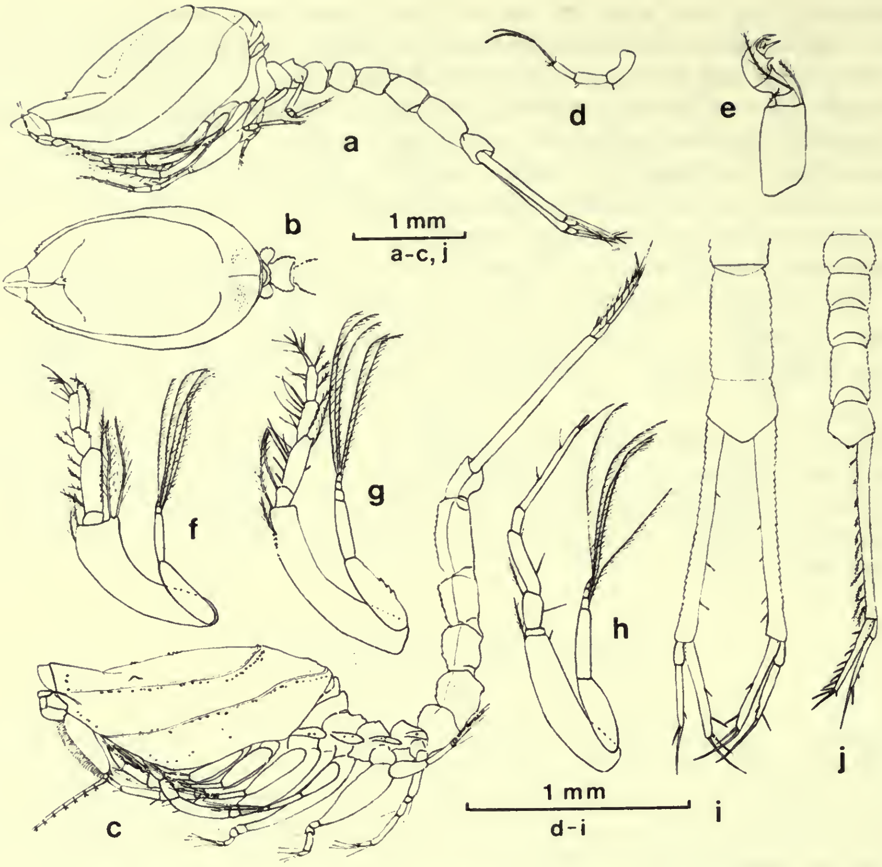

FIG. 20. *Campylaspis bicarinata*. a, ♀ from side ; b, ♀ carapace from above ; c, ♂ from side ; d, ♀ antenna 1 ; e, ♀ maxilliped 2 ; f, ♀ maxilliped 3 ; g, ♀ pereopod 1 ; h, ♀ pereopod 2 ; i, ♀ uropod and end of pleon ; j, ♂ uropod and end of pleon.

Pereopod 1 (fig. 20g) with the basis curved, serrated on the distal lower edge, about as long as the rest of the appendage ; there is a spine on the upper distal end of the merus. Pereopod 2 (fig. 20h) with the basis about two-thirds as long as the remaining segments together ; the dactyl is slender, little tapered, with some setae and one short thick spine distally ; it is very little longer than the carpus and propodus together.

Uropod (fig. 20i) about as long as the last four pleonites combined, the peduncle serrated on its outer edge, more than twice as long as the endopod, which is distinctly longer than the exopod ; the endopod has three thin spines on its inner edge and a longer end spine.

Adult male, length 4·7 mm (fig. 20c, j) : differs in the usual respects from the female. The flagellum of antenna 2 is probably as long as the body including uropods. A male, length 6·0 mm, from the Gay Head – Bermuda transect differs in some minor respects from males from the Dakar – Recife transect, especially in the presence of some small spines dorsally on the carapace and a low tubercle on either side of the frontal area ; it also has a number of blotches of red pigment on the carapace and pereon somites, especially concentrated along the lateral ridges. These, and some small differences in the appendages, however, do not seem to warrant separation of the specimens from the two areas.

TYPE LOCALITY. 0°46′S, 29°28′W–0°46·5′S, 29°24′W, 3459 m. Types deposited in the British Museum (Natural History). Registration numbers : Holotype 1974 : 319 ; Paratypes 1974 : 320.

REMARKS. *C. bicarinata* is fairly near to *C. undata* Sars but the latter species has a well-developed eyelobe with lenses and there are various differences in the appendages ; in particular the dactyl of pereopod 2 is much more slender and proportionately longer in *C. bicarinata* and the peculiar spine at its distal end is not present in *C. undata* but somewhat resembles the distal armature of the dactyl of pereopod 2 in *C. plicata* and *C. bulbosa.*

A moderate number of specimens was obtained at several stations on the Gay Head – Bermuda transect and in the western part of the Dakar – Recife transect, between 834 and 4680 m.

Campylaspis rostrata Calman, 1905

MATERIAL. 43°35·6′N, 3°24·8′W, 860 m, 15.7.1967, 1 ♀; 43°43′N, 3°47·8′W, 641 m, 19.7.1967, 4 ♀♀ ; 46°17·5′N, 4°45·2′W, 1336 m, 24.7.1967, 1 ♂.

DISTRIBUTION. Previously recorded from southwest of the Faroes, southwest of Ireland and the Mediterranean off Monaco, between 220 and 1205 m. The present records from the Bay of Biscay extend its lower depth limit slightly to 1336 m. Calman (1910) records it from the coast of Sudan but this must be a mistake. The latitude and longitude given place the position somewhere south of the Canary Islands.

Campylaspis intermedia Hansen, 1920

MATERIAL. 39°50·5′N, 70°35′W, 823·5 m, 25.5.1961, 1 ♀; 39°54·5′N, 70°35′W, 466·7–508·7 m, 23.5.1962, 1 ♀; 39°46·5′N, 70°43·3′W, 1470–1330 m, 25.8.1964, 36 ♀♀, 12 ♂♂, 4 juv. ; 39°48·7′N, 70°40·8′W, 1102 m, 6.7.1965, 3 ♀♀, 2 ♂♂, 4 juv. ; 39°54·1′N, 70°37′W, 478 m, 6.7.1965, 8 ♀♀ ; 39°56·6′N, 71°03·6′W, 530 m, 5.5.1966, 1 ♀ ; 39°38·5′N, 70°36·5′W–39°39′N, 70°37·1′W, 2178 m, 18.12.1966, 2 ♀♀, 4 juv.

DISTRIBUTION. The only previous records are those of Hansen (1920) from the Davis Strait and south of Jan Mayen in 582 and 679 m. The present records extend its geographical range southwards in the N.W. Atlantic and its depth range to between 467 and 2178 m. It seems to be confined more or less to the continental slope.

Campylaspis submersa sp. nov.

(fig. 21)

Material. 8°02′S, 34°03′W–7°56′S, 34°09′W, 1493 m, 19.2.1967, 2 ♀♀.

Description. Adult female, length 3·4 mm: carapace (fig. 21a, b, c) distinctly less than twice as long as high, nearly oval in outline, with many rather large rounded prominences on the dorsal part; on either side is a shallow indistinct sulcus. The pseudorostrum is blunt, less than a sixth of the total carapace length, with a distinct antennal notch below and an acute antero-lateral angle. The eyelobe is large and broad but without lenses.

Antenna 1 (fig. 21d) with the first segment of the peduncle broad, slightly curved, nearly twice as long as the third segment.

Maxilliped 2 (fig. 21e) with the ischiobasis fairly long, its distal seta normally pinnate; the distal spine of the propodus reaches a little beyond the spines of the dactyl, of which there are three, the middle small. Maxilliped 3 (fig. 21f) with the basis curved, fairly slender and distinctly longer than the remaining segments together; the merus is broadened distally.

Pereopod 1 (fig. 21g) with the basis moderately curved, slender, a little longer than the rest of the appendage; no spines or serrations are present. Pereopod 2 (fig. 21h) with the basis fairly broad, about half as long as the rest of the appendage; the dactyl is tapered to a point, with several slender spines at its end, and is shorter than the carpus and propodus together.

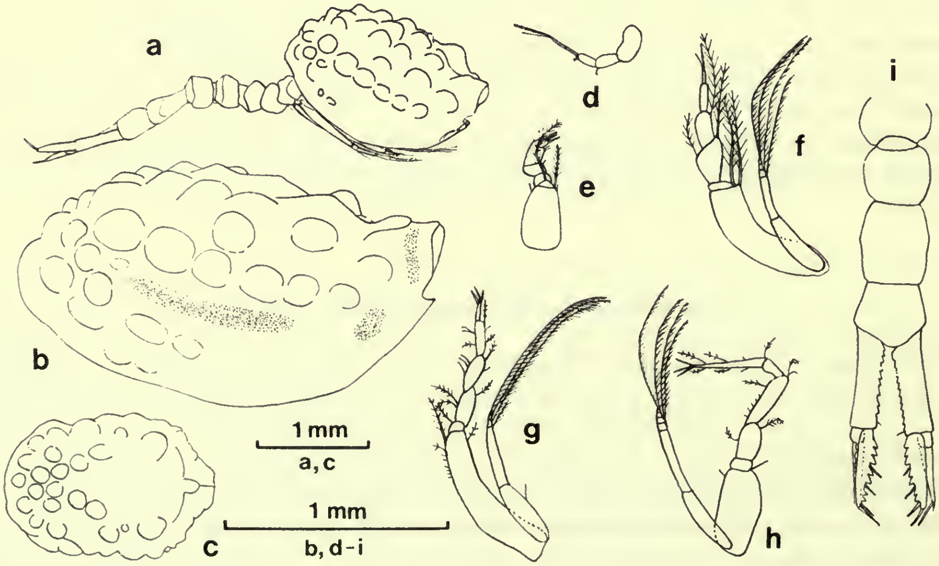

Fig. 21. *Campylaspis submersa* ♀. a, from side; b, carapace from side; c, carapace from above; d, antenna 1; e, maxilliped 2; f, maxilliped 3; g, pereopod 1; h, pereopod 2; i, uropod and end of pleon.

Uropod (fig. 21i) fairly broad, shorter than the last three pleon somites together; the peduncle is serrated on the inner edge and only about a quarter longer than the endopod, which is a little longer than the exopod; the endopod has some strong serrations and three slender spines on the inner edge, with one end spine.

TYPE LOCALITY. 8°02′S, 34°03′W–7°56′S, 34°09′W, 1493 m. Types deposited in the British Museum (Natural History). Registration numbers: Holotype 1974 : 321; Paratype 1974 : 322.

REMARKS. None of the described species of *Campylaspis* has precisely the arrangement of large rounded prominences on the carapace shown by this species, although there are a number with fairly large tubercles, such as *C. globosa* Hansen. This arrangement and the short, rather broad uropods, as well as the relative proportions of some of the appendages, should make recognition easy.

Two specimens only were collected off Recife, Brazil, in 1493 m.

Campylaspis paucinodosa sp. nov.

(fig. 22)

MATERIAL. 39°54·5′N, 70°35′W, 466·7–508·7 m, 23.5.1962, 1 ♀.

DESCRIPTION. Subadult female, length 3·9 mm: carapace (fig. 22a, b) distinctly less than twice as long as high, with a relatively small number of fairly large tubercles confined to the dorsal half and with a shallow excavation on either side. The

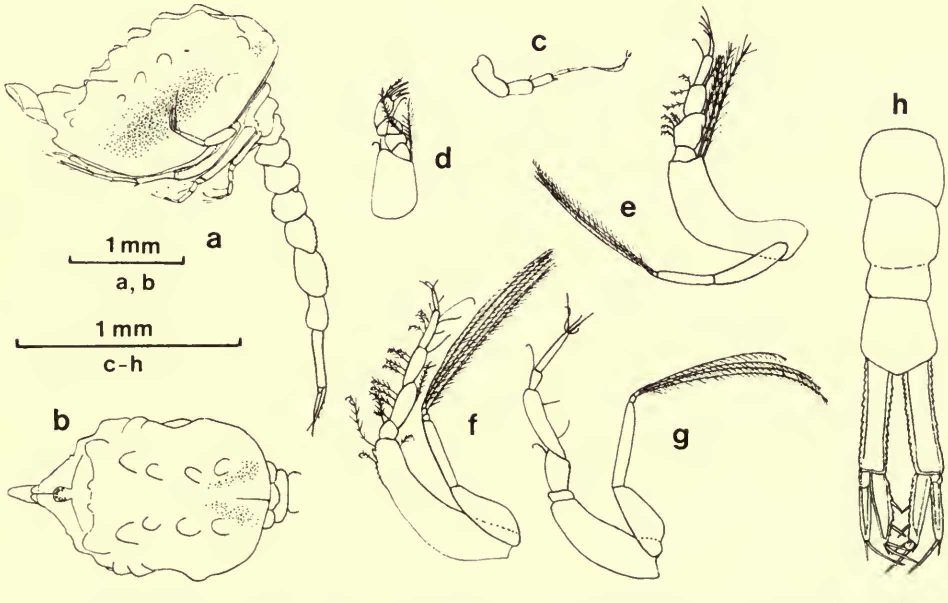

FIG. 22. *Campylaspis paucinodosa* immature ♀. a, from side; b, carapace from above; c, antenna 1; d, maxilliped 2; e, maxilliped 3; f, pereopod 1; g, pereopod 2; h, uropod and end of pleon.

pseudorostrum is inclined slightly upwards and fairly acutely pointed from the side, truncated from above, with a well-defined antennal notch below and a distinct but rounded antero-lateral angle. The eyelobe is large and prominent and has visible lenses.

The fourth and fifth pleonites are serrated dorsally.

Antenna 1 (fig. 22c) with the first segment of the peduncle broad basally, slightly curved, about twice as long as the third.

Maxilliped 2 (fig. 22d) with the basis fairly broad, its distal seta normally pinnate; the terminal spine on the propodus is fairly long and slender; the dactyl has two end spines of equal length. Maxilliped 3 (fig. 22e) with the basis strongly curved, longer than the rest of the appendage; the merus is fairly broad but none of the segments have spines or serrations.

Pereopod 1 (fig. 22f) with the basis a little longer than the remaining segments together, with some serrations on the distal lower edge. Pereopod 2 (fig. 22g) with the basis about two-thirds as long as the rest of the appendage; the dactyl is short, scarcely tapering, much shorter than the carpus.

Uropod (fig. 22h) short, about as long as the last two pleonites together; the peduncle is serrated on either edge, about one-and-a-half as long as the endopod, which is scarcely longer than the exopod; the endopod has some serrations and three fairly stout spines on its inner edge and two unequal end spines.

TYPE LOCALITY. 39°54·5′N, 70°35′W, 467–509 m. Type deposited in the British Museum (Natural History). Registration number: Holotype 1974 : 323.

REMARKS. *C. paucinodosa* shows some resemblance to *C. horrida* Sars but it has a smaller number of tubercles and is without dorso-lateral projections on the pereonites and anterior pleonites; the uropods are also much shorter and the relative proportion of the peduncle to the endopod much smaller than in *C. horrida*.

Calman (1912) doubtfully referred a dried and broken specimen from 428 fathoms in nearly the same locality as that for *C. paucinodosa* to *C. horrida*. It is likely that it was *C. paucinodosa*, and not *C. clavata*, as suggested by Lomakina (1958).

A single specimen was obtained south of Gay Head in 467–509 m.

Campylaspis horridoides Stephensen, 1915
(fig. 23)

MATERIAL. 43°35·6′N, 3°24·8′W, 860 m, 15.7.1967, 3 ♀♀, 1 ♂, 1 juv.; 38°27′N, 4°08′E, 2447 m, June 1970, 1 ♀.

DISTRIBUTION. Previously recorded only from the Mediterranean south of Sardinia in 1227 m this species is now recorded also from the Bay of Biscay and its depth range between 860 and 2447 m.

REMARKS. Although Stephensen's (1915) figures are adequate there is one character which he omits to mention and which may be useful for identifying the species. This is the rather broad suture visible from above along the mid-dorsal line (fig. 23) which differs in appearance from closely related species such as

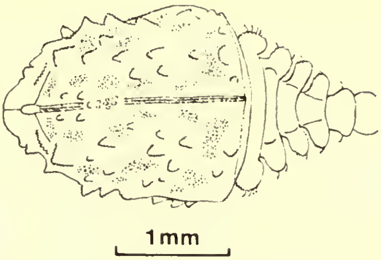

FIG. 23. *Campylaspis horridoides* ♀. Carapace and pereon from above.

C. squamifera Fage. Dr Torben Wolff of Universitetets Zoologiske Museum, København, has kindly allowed me to examine Stephensen's original specimens which I have checked for this character and from which I have selected lectotypes.

Campylaspis squamifera Fage, 1929

MATERIAL. 43°35·6′N, 3°24·8′W, 860 m, 15.7.1967, 5 ♀♀, 1 ♂, 3 juv.; 43°43′N, 3°47·8′W, 641 m, 19.7.1967, 3 ♀♀, 5 ♂♂, 19 juv.

DISTRIBUTION. Known previously from a single specimen dredged in the south of the Bay of Biscay from 4380 m, those recorded here are from considerably lesser depths in the more northerly part of the Bay.

Campylaspis glebulosa sp. nov.
(fig. 24)

MATERIAL. 0°03′S, 27°48′W, 3730–3783 m, 13.2.1967, 1 ♂; 0°46′S, 29°28′W–0°46·5′S, 29°24′W, 3459 m, 14.2.1967, 1 ♀; 7°58′S, 34°17′W–7°50′S, 34°17′W, 943–1007 m, 20.2.1967, 1 ♀; 8°03′S, 34°23′W–8°02′S, 34°25′W, 587 m, 21.2.1967, 1 ♀.

DESCRIPTION. Adult female, length 4·5 mm: carapace (fig. 24a, b) a little more than one-and-a-half as long as high, well elevated, with fairly numerous tubercles, most of which are serrated, and an ill-defined sulcus on either side; there is a short transverse ridge across the middle of the frontal area. The pseudorostrum is less than a sixth of the total carapace length, bluntly pointed from the side, with a slightly excavated antennal notch below and a slightly projecting antero-lateral angle. The eyelobe is fairly large but without lenses.

The pereon and anterior pleon somites have serrated low dorsal projections.

Antenna 1 (fig. 24d) with the basal segment of the peduncle curved, nearly three times as long as the third.

Maxilliped 2 (fig. 24e) with the ischiobasis long, its terminal seta fairly short and pinnate distally but not thickened; terminal propodal spine about as long as the spines of the dactyl, of which there are three, the middle very small. Maxilliped 3 (fig. 24f) with the basis curved, distinctly longer than the rest of the appendage; the segments are not broad, the merus and carpus with some strong spines on the upper edge.

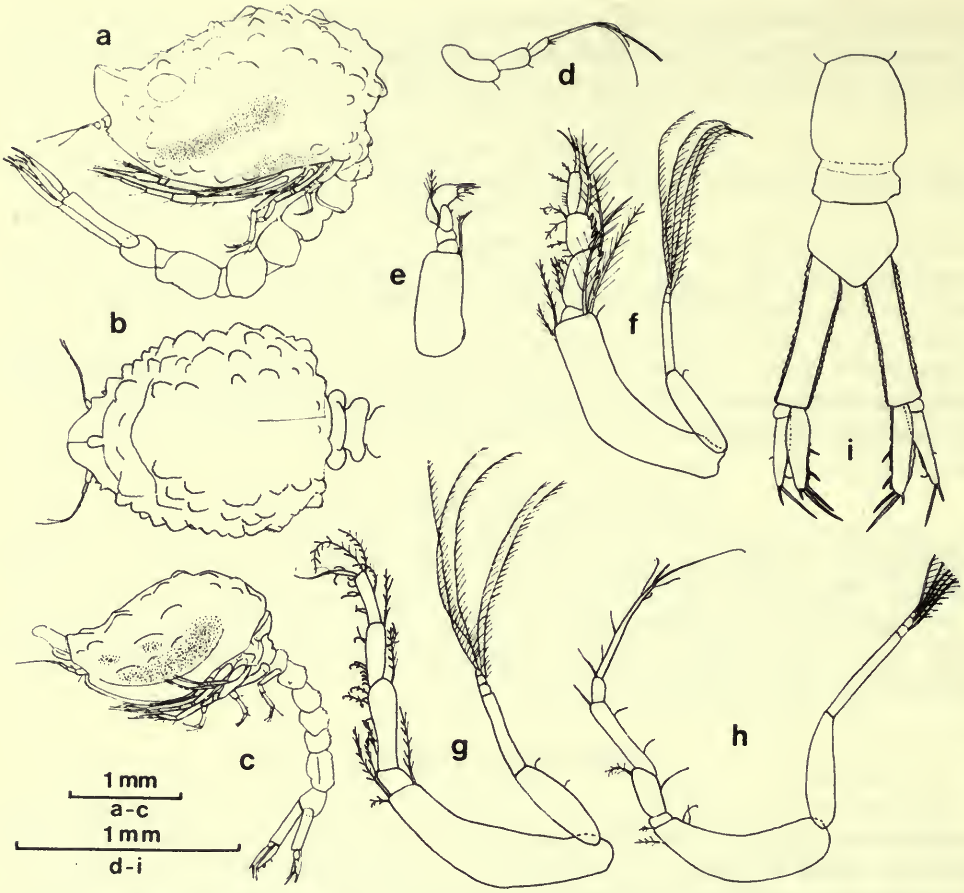

Fig. 24. *Campylaspis glebulosa*. a, ♀ from side; b, ♀ carapace from above; c, immature ♂ from side; d, ♀ antenna 1; e, ♀ maxilliped 2; f, ♀ maxilliped 3; g, ♀ pereopod 1; h, ♀ pereopod 2; i, ♀ uropod and end of pleon.

Pereopod 1 (fig. 24g) with the basis moderately curved, a little longer than the rest of the appendage. Pereopod 2 (fig. 24h) with the basis about two-thirds as long as the rest of the appendage; the dactyl is tapered but not pointed, with long slender terminal spines, and is almost as long as the carpus and propodus together.

Uropod (fig. 24i) about as long as the last two pleonites together; the peduncle is serrated on either edge and more than one-and-a-half as long as the endopod, which is equal in length to the exopod; the endopod has some serrations on either edge and three fairly slender spines on the inner edge, with two unequal end spines.

Type locality. 0°46′S, 29°28′W–0°46·5′S, 29°24′W, 3459 m. Types deposited in the British Museum (Natural History). Registration numbers: Holotype 1974 : 324; Paratype 1974 : 325.

REMARKS. *C. glebulosa* quite closely resembles *C. squamifera*, but has fewer tubercles, especially on the sides of the carapace, and lacks the dorso-lateral processes and strong serrations present on the pereon and pleon of the latter species. There are also many differences in the appendages, especially the comparative lack of teeth or serrations in *C. glebulosa* and the much longer basis of pereopod 2 compared with the rest of the appendage. From *C. globosa* Hansen this species may be distinguished, among other characters, by the comparative shortness of the uropods, which in *C. globosa* are as long as the last three pleonites.

A few specimens were obtained at several stations in the western part of the Dakar – Recife transect, in 587–3783 m.

Campylaspis torulosa sp. nov.

(fig. 25)

MATERIAL. 36°23′N, 67°58′W, 4680 m, 23.8.1964, 18 ♀♀, 4 ♂♂; 36°24·4′N, 67°56′W, 4749 m, 4.7.1965, 3 ♀♀, 6 ♂♂, 2 juv.; 36°20′N, 67°56′W, 4694 m, 13.12.1965, 1 ♀; 37°24′N, 65°54′W–37°26′N, 65°50′W, 4825 m, 23.8.1966, 1 ♀, 4 ♂♂, 3 juv.

DESCRIPTION. Adult female, length 5·2 mm: carapace (fig. 25a, b) about twice as long as high, evenly rounded dorsally, somewhat produced backwards over the anterior pereonites, with many fairly large tubercles or blunt spines set in irregular rows, leaving a fairly small area free from tubercles on either side; the frontal area is crossed by two poorly defined transverse ridges. The pseudorostrum is short and obtuse, less than a seventh of the total carapace length, with a trace of an antennal notch below, defined posteriorly by two blunt teeth. The eyelobe is of moderate size, without lenses.

The pereon and the first five pleon somites have blunt lateral projections and there are some small tubercles on the dorsum of the fifth pleonite.

Antenna 1 (fig. 25c) with the segments of the peduncle fairly stout, the first curved and nearly three times as long as the third.

Maxilliped 2 (fig. 25d) with the ischiobasis broad and truncated at the base; the carpus has a small tooth on the distal inner edge; the propodal process reaches beyond the spines of the dactyl, of which there are two of approximately equal length. Maxilliped 3 (fig. 25e) with the basis much longer than rest of appendage; the ischium has some teeth on the lower edge and there are a number of teeth on the lower edge of the merus, which also has a sharp tooth on the upper edge distally; there are several sharp teeth on the upper edge of the carpus; the ischium and merus are fairly broad.

Pereopod 1 (fig. 25f) with the basis distinctly longer than rest of appendage, serrated distally on both edges. Pereopod 2 (fig. 25g) with the basis broad, less than three-quarters as long as the remaining segments together, serrated distally on either edge; the dactyl is little tapered, with a blunt end, about as long as the carpus and propodus together.

Uropod (fig. 25h) broad, a little shorter than the last three pleonites together, the peduncle serrated on either edge and with some short setae on the inner edge, only about one-and-a-quarter as long as the endopod, which is a little longer than the

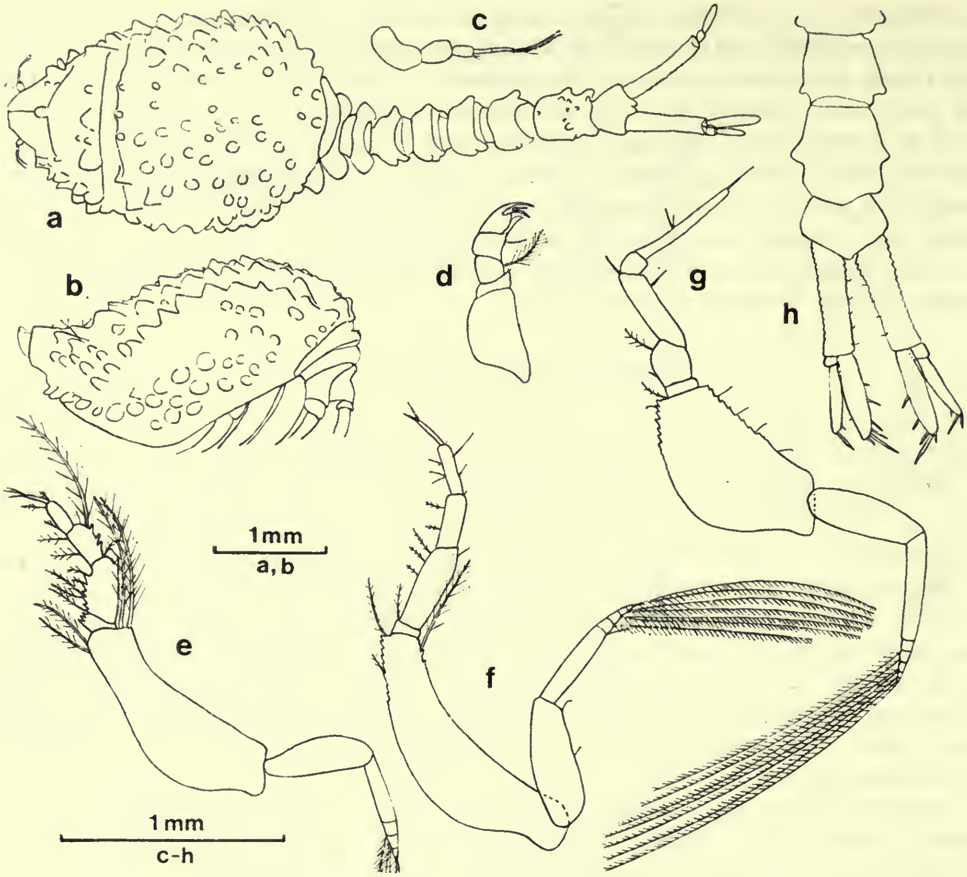

FIG. 25. *Campylaspis torulosa* ♀. a, from above ; b, carapace from side ; c, antenna 1 ; d, maxilliped 2 ; e, maxilliped 3 ; f, pereopod 1 ; g, pereopod 2 ; h, uropod and end of pleon.

exopod ; the endopod has three or four spines on the inner edge and two unequal end spines.

TYPE LOCALITY. 37°24′N, 65°54′W–37°26′N 65°50′W, 4825 m. Types deposited in the British Museum (Natural History). Registration numbers : Holotype 1974 : 326 ; Paratypes 1974 : 327.

REMARKS. *C. torulosa* seems to be closely related to *C. papillata* Lomakina but the arrangement of the tubercles on the carapace is somewhat different, while in *C. papillata* the dactyl of pereopod 2 is more tapered and the endopod of the uropod is narrower and has a greater number of spines on its inner edge. It also resembles *C. squamifera* but has many more tubercles on the dorsum of the carapace than that species.

The species was obtained on several occasions on the deeper parts of the Gay Head – Bermuda transect from the abyssal plain, between 4680 and 4825 m.

Campylaspis verrucosa G. O. Sars, 1866

MATERIAL. 43°40·8'N, 3°35·2'W, 1739 m, 16.7.1967, 3 ♂♂; 43°43'N, 3°47·8'W, 641 m, 19.7.1967, 4 ♀♀, 1 ♂♂.

DISTRIBUTION. Recorded from the N.E. Atlantic from the Lofotens to the coast of Portugal and from the Mediterranean, between 100 and 1100 m. The present records from the Bay of Biscay increase the lower limit of known occurrence to 1739 m.

Campylaspis globosa Hansen, 1920

MATERIAL. 39°26'N, 70°33'W, 2496 m, 21.8.1964, 20 ♀♀; 38°46'N, 70°06'W, 2886 m, 21.8.1964, 1 ♀; 39°55·2'N, 70°39·5'W, 498 m, 27.4.1966, 11 ♀♀, 6 ♂♂; 39°56·6'N, 71°03·6'W, 530 m, 5.5.1966, 1 ♀.

DISTRIBUTION. Previously recorded only from the Davis Strait in 2626 m. As with *C. intermedia*, which has much the same geographical range, its range is extended to the south and its upper depth limit to 498 m. It appears to extend to greater depths than *C. intermedia*.

Campylaspis multinodosa sp. nov.
(fig. 26)

MATERIAL. 23°00'S, 12°45'E, 1007–1014 m, 16.5.1968, 12 ♀♀, 1 ♂; 23°05'S, 12°31·5'E, 1546–1559 m, 17.5.1968, 1 ♀, 2 juv.; 23°02'S, 12°19'E, 2117–2154 m, 17·5·1968, 1 ♀, 2 ♂♂.

DESCRIPTION. Adult female, length 3·9 mm: carapace (fig. 26a, b) twice as long as high, with many small tubercles dorsally and on the sides, some of which are acute, especially on the pseudorostrum and just below it; on either side is a fairly small shallow excavation. The pseudorostrum is more than a sixth of the total carapace length, truncate in front, with a well-defined antennal notch and antero-lateral angle below it. The eyelobe is fairly large but without lenses.

The last pereonite and the first five pleonites have paired dorso-lateral teeth.

Antenna 1 (fig. 26d) with the segments of the peduncle slender, the basal segment slightly curved and less than one-and-a-half as long as the third.

Maxilliped 2 (fig. 26e) with the ischiobasis fairly long, serrated on its distal outer edge, with its distal seta normally pinnate; the carpus has a few serrations on the outer edge and the propodus a tooth on the inner edge and a slender end spine; the dactyl has two spines. Maxilliped 3 (fig. 26f) with the basis slender, serrated on either edge distally, much longer than the remaining segments together; these are not widened and the merus, carpus and propodus are serrated on the lower edge; the dactyl is small.

Pereopod 1 (fig. 26g) with the basis about as long as the rest of the appendage, serrated on its distal lower edge; there are one or two serrations on the lower edge of the ischium. Pereopod 2 (fig. 26h) with the basis little more than half as long as the rest of the appendage, serrated along its distal upper edge; the merus is serrated distally on both edges and the carpus proximally on the upper edge; the dactyl is

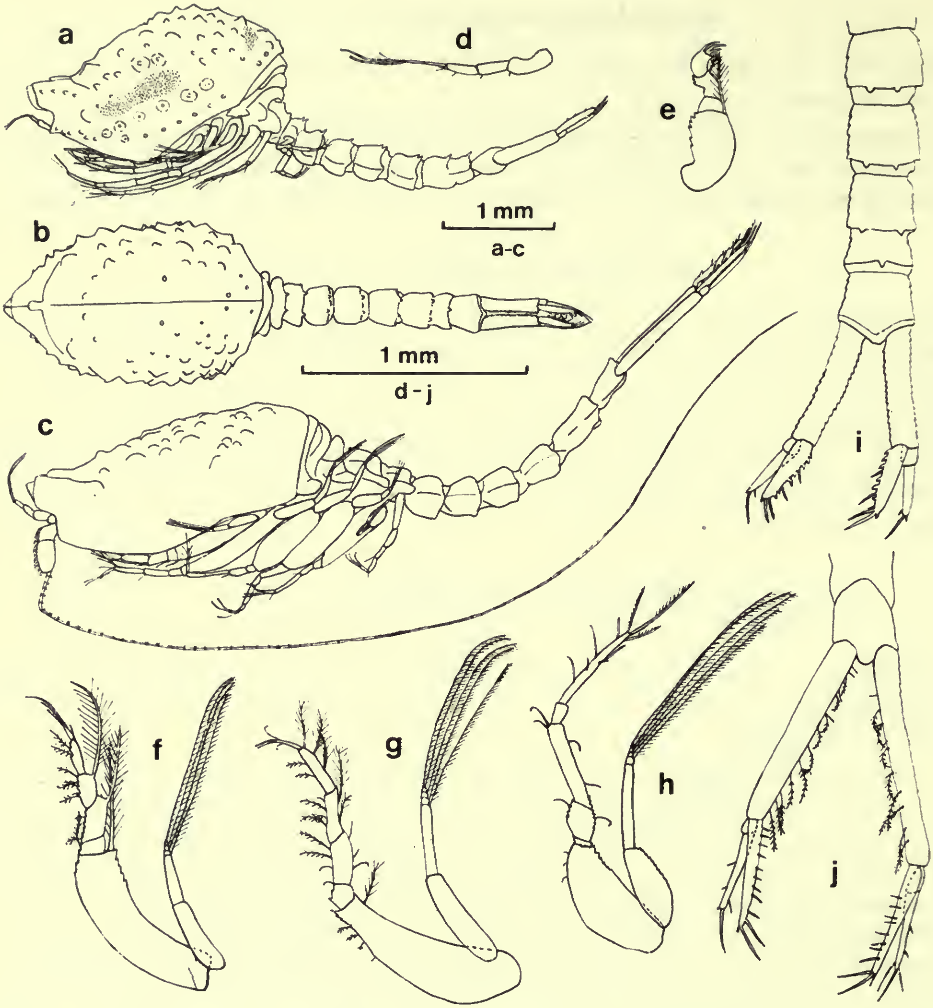

FIG. 26. *Campylaspis multinodosa.* a, ♀ from side ; b, ♀ from above ; c, ♂ from side ; d, ♀ antenna 1 ; e, ♀ maxilliped 2 ; f, ♀ maxilliped 3 ; g, ♀ pereopod 1 ; h, ♀ pereopod 2 ; i, ♀ uropod and end of pleon ; j, ♂ uropod and end of pleon.

not tapered and has several fairly long pinnate end spines ; it is a little shorter than the carpus and propodus together.

Uropod (fig. 26i) rather longer than the last two pleon somites together, the peduncle serrated on either edge and about one-and-three-quarters as long as the endopod, which is a little longer than the exopod ; the endopod has some stout serrations and three spines on the inner edge, with two unequal end spines.

Adult male, length 5·3 mm (fig. 26c, j) : differs from the female in the usual characters. The sides of the carapace are smoother and there are no dorso-lateral teeth on the pleon somites. The second antennal flagellum reaches to the end of the uropods and these are more slender and have more setae and spines but are little serrated.

TYPE LOCALITY. 23°00'S, 12°45'E, 1007–1014 m. Types deposited in the British Museum (Natural History). Registration numbers: Holotype 1974 : 328; Paratypes 1974 : 329.

REMARKS. *C. multinodosa* shows a considerable resemblance to *C. antarctica* Calman. The latter has several teeth on the outer side of the carpus of maxilliped 3 and the dactyl of pereopod 2 is longer than the carpus and propodus together, but otherwise it is difficult to separate them and the two are very closely related and perhaps identical.

A moderate number of specimens were captured at several stations off S.W. Africa in 1007–2154 m.

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A NEW FAMILY, GENUS AND SPECIES OF BAT (MAMMALIA : CHIROPTERA) FROM THAILAND

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ZOOLOGY Vol. 27 No. 7
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JOHN EDWARDS HILL

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By J. E. HILL

INTRODUCTION

WHILE Curator of Terrestrial Vertebrates at the Centre for Thai National Reference Collections, Bangkok, the late Kitti Thonglongya became especially interested in the bats of Thailand. His enthusiasm has led in the past few years to the discovery of two new species (*Rhinolophus marshalli* Thonglongya, 1973, *Hipposideros lekaguli* Thonglongya & Hill, 1974) in Thailand, and has added other species (*Rhinolophus paradoxolophus, Myotis annectans, Pipistrellus cadornae*) to the Thai fauna (Thonglongya, 1973 ; Hill & Thonglongya, 1972). He was also responsible for the discovery in the collections of the Bombay Natural History Society of an undescribed genus and species of Indian fruit bat (*Latidens salimalii* Thonglongya, 1972). In the latter part of 1973 he obtained specimens in southern Thailand which he thought might represent an unknown genus and species justifying perhaps the establishment of a further higher category within the Microchiroptera. Specimens sent to the British Museum (Natural History), London, fully confirmed his initial opinion, and showed the new genus to differ sufficiently from the established categories of the Microchiroptera to warrant the proposal of a further family.

Originally, the intention had been to describe this remarkable new bat in a joint paper. With this in view, a detailed comparative study was begun in London to establish and evaluate its diagnostic features, many already recognized by Kitti Thonglongya during his preliminary examination in Thailand. As a result of his sudden and untimely death in February 1974, the Applied Scientific Research Corporation of Thailand, through Dr Prasert Lohavanijaya, the Director of the Centre for Thai National Reference Collections, has entrusted me with the preparation of the account. In these circumstances I deem it an honour and a privilege to recognize the contribution made by my former friend and colleague by associating his name with the most outstanding and significant discovery that he made in his studies of the bats of his country.

DIAGNOSES AND DESCRIPTION

CRASEONYCTERIDAE fam. nov.

DIAGNOSIS. Similar in some respects to the Rhinopomatidae and to the Emballonuridae but second finger with one very short bony phalange, usually ankylosed to the metacarpal and with an equally short cartilaginous tip. As in these families the premaxillae not fused to surrounding or adjacent parts. However, they are united anteriorly to enclose a large anterior palatal vacuity and posteriorly to surround the narial aperture ; palatal branches short, solidly ankylosed throughout their length to form a posteriorly projecting, tapered spine extending across about one half or less of the anterior palatal vacuity which it thus divides into two posteriorly confluent foramina ; narial branches extending upwards to lie posteriorly on the surface of the maxillae and nasals as a thin, laminar, posteriorly rectangular plate, with no trace of a median suture, the inner margin of this structure forming a narrow, sub-tubular, anteriorly directed flange which borders the lateral and upper parts of the narial opening. Humerus with trochiter or greater tuberosity as large as trochin or lesser tuberosity, trochiter extending proximally beyond the head of the humerus ; a shallow supraglenoid recess between the proximal base of the head of the humerus and the base of the trochiter ; anterior face of proximal part of shaft of humerus flattened in its central part, lacking any median deltoid ridge, instead a slightly elevated area at the base of the trochiter, extending distally along the proximal part of the shaft as a short dorsal flange supporting the trochiter, with a similar but shorter ventral flange supporting the trochin ; capitellum slightly displaced from line of shaft ; epitrochlea or medial process a little less than half as wide as distal articular surface, with small epitrochlear or distal spinous process. Sternum not especially modified ; shoulder girdle normal ; last cervical vertebra not fused with first thoracic ; lower three thoracic vertebrae fused, their boundaries faintly visible ; lumbar vertebrae except last two solidly ankylosed, the last two free ; sacral vertebrae fused, their boundaries obliterated or nearly so. Pelvis small, weak, ascending ramus of pubis short, without definite acicular or pubic spine, the ventral ramus delicate, very thin ; ischium with ascending ramus similarly thin and delicate, these structures easily lost in preparation ; fibula thread-like, extending about halfway along the tibia.

CRASEONYCTERIS gen. nov.

DIAGNOSIS. Most nearly resembling *Rhinopoma*, the sole genus of the Rhinopomatidae, but differing as above and further in normal, slightly crescentic nostrils which are not slit-like or valvular although as in *Rhinopoma* they open directly anteriorly in the face of a thickened, vertical narial pad or plate ; ridge-like dermal protrusion surmounting narial plate lower and narrower ; ears not joined anteriorly by a band of integument ; tragus narrowed and rounded at the tip, not truncate, and with an oblate swelling in the centre of its anterior margin. Distal phalange of third digit very long, reflexed beneath wing in specimens preserved in alcohol ; distal phalange of fourth digit similarly reflexed ; no external tail, the uropatagium not shortened. Braincase more inflated and more globular than in *Rhinopoma* ; postorbital region less markedly constricted ; lateral rostral swellings less inflated, not projecting anteriorly to surpass the narial aperture which slopes posteriorly and is not nearly vertical as in *Rhinopoma* ; zygomata less expanded ; coronoid process low, below height of articular process. Dentition similar to that of *Rhinopoma*, the dental formula i $\frac{1}{2}$, c $\frac{1}{1}$, pm $\frac{1}{2}$, m $\frac{3}{3}$ = 28 as in that genus, but upper incisors relatively much larger and third upper molar a little more reduced.

TYPE SPECIES. *Craseonycteris thonglongyai* sp. nov.

REMARKS. The name of the new genus is derived from *κρᾶσις* or *κρᾶσέως*, a mixing or blending, with *νυκτερὶς*, a bat, in allusion to the combination of features presented by this notable discovery. Since the genus is proposed to include only the type species, one description may serve for both.

Craseonycteris thonglongyai sp. nov.

HOLOTYPE. Thai National Reference Collections No. 54-3871. Adult ♂. Cave near the Forestry Station, Ban Sai Yoke, Kanchanaburi, Thailand, 14°26′ N, 98°51′ E. Collected 8 December 1973 by Kitti Thonglongya. Original number KT 5710. In alcohol, skull extracted.

OTHER MATERIAL. Thai National Reference Collections (in alcohol unless stated): ♂♂ Nos. 54-3213 (skull, left humerus, left femur extracted, skull not seen), 26 October 1973; 54-3865 (disarticulated skeleton), 54-3866–3870 (skulls extracted), 54-3872–3873, 54-3874–3875 (skulls extracted), 54-3876, 54-3884 (skull extracted), 54-3886, 54-3887–3888 (skulls extracted), 54-3889, 8 December 1973; ♀♀ Nos. 54-3230 (skull extracted, right fibula exposed), 28 October 1973; 54-3877, 54-3878–3881 (skulls extracted), 54-3882–3883, 54-3885, 8 December 1973. Collected by Kitti Thonglongya at or near the type locality.

This account is based on the specimens listed. A total of fifty-two numbers is allocated to specimens of this bat in the field catalogue maintained by Kitti Thonglongya: those not examined in the preparation of this study have remained in the Thai National Reference Collections and include skins, skulls, skeletons and specimens preserved in alcohol (J. T. Marshall, in litt.). The entire representation came from one or other of two caves near the Forestry Station, Ban Sai Yoke, probably about 2 km along the Kwae Noi River past its junction with the Huay Mae Nam Noi River (J. T. Marshall, in litt.). Specimens collected in October 1973 came apparently from 'Tham Wang Phra', those in December from 'Namtok Sai Yoke'. The final disposition of the series examined at the British Museum (Natural History) has yet to be decided but it is expected that the specimens will remain in London for an indefinite period, some permanently.

DESCRIPTION. A very small bat (length of forearm 22–26 mm), dorsally greyish brown, ventrally rather greyer, some specimens with a slight reddish tinge dorsally (from alcohol), membranes dark. Muzzle (Fig. 1) rather suiform, slightly swollen laterally; anterior part of chin similarly swollen, the swelling faintly divided medianly; anteriorly muzzle with a thickened, fleshy vertical narial pad or plate surmounted by a low dermal ridge extending across the central part of the narial pad; nostrils wide, slightly crescentic, opening directly anteriorly in the face of the narial pad, sharply inclined to the horizontal, separated by a relatively wide internarial septum which broadens above the nostrils to form the base of the low dermal ridge. Shallow grooves extend upwards from the upper corner of each nostril to separate the dermal ridge from the lateral elements of the narial pad; shallow depressions extend downwards from the lateral margins of the internarial septum towards the upper lip; central part of lower lip raised by a smooth, naked swelling

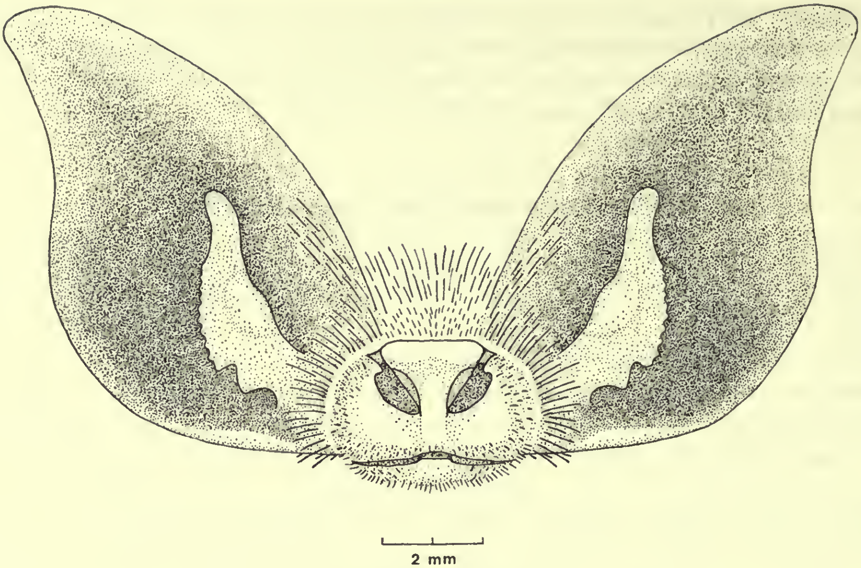

FIG. 1. *Craseonycteris thonglongyai*. Head.

immediately anterior to and extending across the lower incisors. Narial pad and median anterior part of lower lip naked ; lateral swellings of muzzle and of chin sparsely covered with short, rather stiff hairs, underside of chin and throat only lightly furred.

Eyes small, largely concealed in fur ; ears (Fig. 1) very large and rather membranaceous, reaching beyond the tip of the muzzle when laid forward. Ear rounded at the tip, anterior margin originating just above eye, without basal lobe, convex, posterior margin moderately concave just beneath tip, then straight, proximal half strongly convex, inserted quadrately just behind angle of mouth, antitragus poorly developed, little more than a thickening of the ear membrane. Outer surface of conch with a few sparse hairs in its proximal half, inner surface with a diffuse band of sparse hairs posterior and parallel to the proximal part of its anterior margin, a few sparse hairs in its distal part.

Tragus (Fig. 1) a little less than one half the length of the ear, basally narrow beneath a small, more or less triangular posterior basal lobe, then broadly expanded, its greatest width at about one half its length, narrowing abruptly to a rounded tip. Anterior part of tragus with distinct oblate thickening about halfway along its length, the thickened area extending across one half of the width of the tragus at this point. Tragus with anterior margin slightly concave proximally, then at the oblate thickening slightly convex beneath a shallow concavity, distal part of margin slightly convex to tip ; posterior margin slightly concave distally, then convex and serrated at the widest part of the tragus, curving abruptly, almost angularly to a shallow rounded emargination just above the posterior basal lobe.

Propatagium or antebrachium broad, originating proximally at a point level with the shoulder joint, extending distally to the distal end of the first metacarpal.

Thumb short, with well-developed claw; membrane between thumb and second metacarpal broad proximally, anchored to the end of the first metacarpal, tapering to a distal termination at a point about halfway along the second metacarpal. Second digit free anteriorly in its distal part, with long metacarpal and one very short bony phalange, usually fused to the metacarpal, the junction visible under relatively high magnification, often marked by a slight broadening of the metacarpal, the digit tipped by a tapered cartilage which is approximately equal in length to the short bony phalange. Membrane lying between second and third digits terminating distally about one quarter or a little more along the length of the second phalange of the third digit from its junction with the first phalange. Third digit with two phalanges, no trace of a third, its metacarpal shorter than the metacarpal of the second digit, the second phalange very long, about three times as long as the first phalange and approximately equal in length to the third metacarpal, strongly reflexed beneath wing in specimens preserved in alcohol. Metacarpal of fourth digit a little longer than that of third digit but shorter than second metacarpal, its first phalange very short, in length about one sixth that of the associated metacarpal, second phalange long, about three times the length of the first phalange, slightly reflexed beneath wing. Metacarpal of fifth digit about as long as fourth metacarpal,

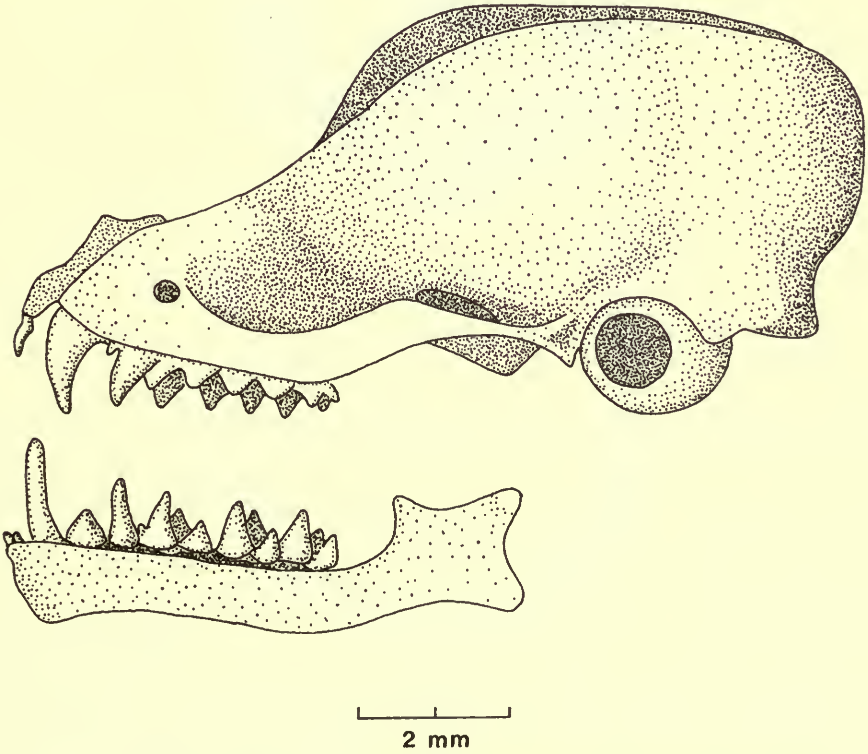

FIG. 2. *Craseonycteris thonglongyai.* Holotype. Lateral aspect of skull.

its first phalange short, about one quarter the length of its metacarpal, the second phalange slightly exceeding the first in length.

No external tail, uropatagium moderate, narrow proximally between upper part of legs to knees, wider distally, its posterior margin slightly curved, terminating medianly at a line a little beyond halfway from knees to ankles, calcar absent, membranes inserted 3–4 mm above the ankle ; a few short hairs on the ventral surface of the endopatagium, clustered at and about the distal end of the humerus, fur not extending on to the uropatagium. Foot long, narrow and slender, the phalangeal formula 2–3–3–3–3, the toes subequal in length, with a few long hairs on the dorsal surface. A rounded glandular swelling at base of underside of throat, well developed and prominent in males, much less so or absent in females. Penis relatively massive, short and broad, moderately covered with short hairs, preputial

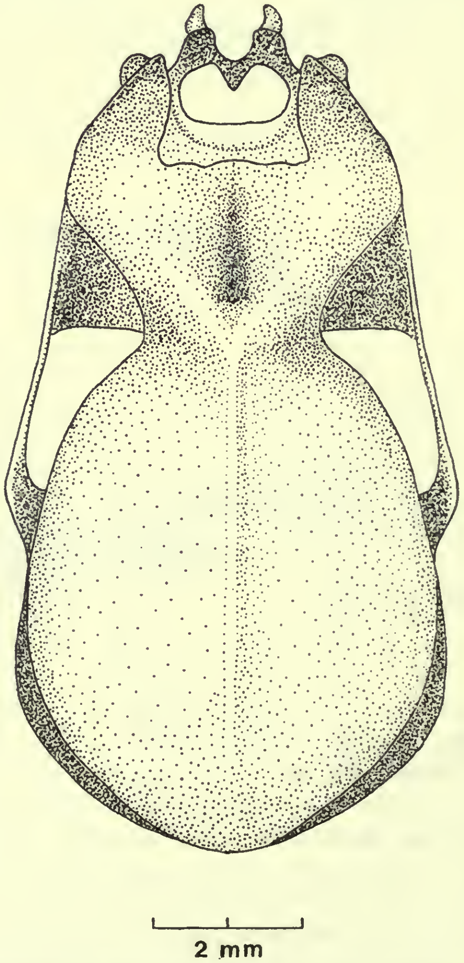

Fig. 3. *Craseonycteris thonglongyai*. Holotype. Dorsal aspect of skull.

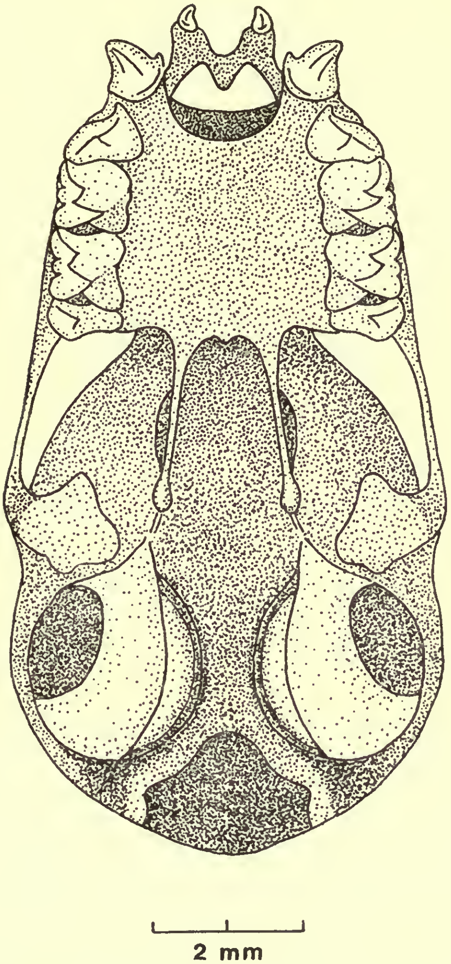

FIG. 4. *Craseonycteris thonglongyai.* Holotype. Ventral aspect of skull.

opening small, rounded ; vulva transverse, set in a fleshy elevation. One pair pectoral and one pair pubic nipples, the latter closely set and situated just anterior to the genital eminence.

Skull (Figs. 2–5) very small (condylobasal length 9·5–10·1 mm) with slightly inflated, globose braincase ; no lambdoid crests ; prominent sagittal crest extending from rear of braincase to frontal region immediately above narrowest postorbital point, its crest slightly higher frontally than posteriorly ; postorbital region not especially constricted. Rostrum wide, laterally expanded ; no postorbital processes or evident supraorbital ridges ; combined nasals wider than long ; lateral rostral swellings well developed and prominent, not extending laterally to project beyond the narial aperture at its sides, swellings separated dorsally by a narrow median rostral depression, deeper posteriorly than anteriorly ; narial opening sloping posteriorly,

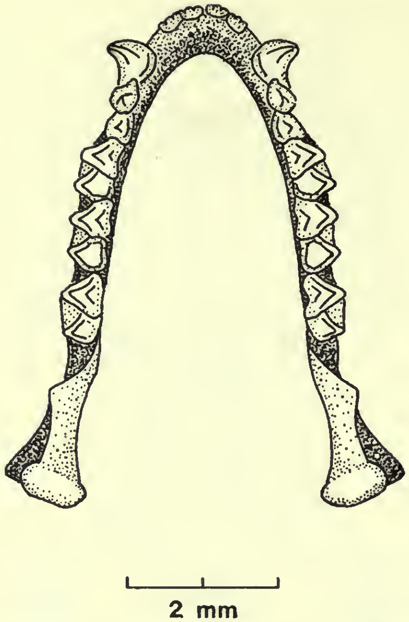

FIG. 5. *Craseonycteris thonglongyai.* Holotype. Dorsal aspect of mandible.

flanked by the lateral rostral swellings. Premaxillae not fused to adjoining parts but completely united ; palatal branches small, totally co-ossified with no trace of a suture, anteriorly a U-shaped emargination between the incisors ; posteriorly the fused palatal branches form a narrow, tapered spike extending across about one half or a little less of the large anterior palatal foramen ; narial branches exceptionally developed to extend upward to the apex of the narial aperture where they are totally fused, forming a thin lamina or plate, rectangular posteriorly, lying on the maxillae and nasals, its inner edge produced anteriorly to form a thin, sub-tubular flange around the lateral and upper parts of the narial opening ; entire premaxillary structure firmly connected by tough tissue to the rear of the narial pad which apparently it serves to support. Anteorbital foramen small ; zygoma unexpanded, slender but with well-developed, rounded jugal process ; palate short, wide, with large anterior foramen closed anteriorly by the premaxillae, its posterior wall extending along a line lying just behind the anterior faces of the upper premolars (pm^{4-4}), partially divided medianly by the spike-like rearward extension of the fused palatal branches of the premaxillae ; maxillary toothrows slightly curved anteriorly ; palate terminating posteriorly on a line slightly in advance of the posterior faces of the third upper molars (m^{3-3}). Mesopterygoid fossa not especially narrow, its width a little less than one third of the external width across m^3–m^3 ; no bony post-palate, the palation a little behind a line joining the posterior faces of m^{3-3} ; pterygoid wings moderately developed, divergent ; no basioccipital pits ; tympanic bullae relatively large, flattened on the inner face. Coronoid process low, its tip below the level of the articular process, angular process slightly deflected.

Soft palate (Fig. 6) with six transverse ridges, the first curved on each side to the median line, second ridge nearly straight, third more definitely incurving to median line, ridges four and five slightly less curved, sixth ridge straight ; first ridge with shallow median division, ridges two to five with small median notch.

Dental formula i $\frac{1}{2}$, c $\frac{1}{1}$, pm $\frac{1}{2}$, m $\frac{3}{3}$; tips of upper incisors (i$^{2-2}$) slightly convergent, i^2 relatively large, separated rather widely from canine, flattened antero-posteriorly, longer than wide, with posteriorly a strong basal cingulum, the cusp acutely triangular in frontal aspect. Upper canine with moderately tall, slender shaft, its base triangular with narrow internal cingulum and small but prominent antero-internal cusp, readily visible from the front. Upper premolar (pm^4) large, with wide lingual shelf and prominent anterior cingulum cusp, easily seen from the side, the posterior margin of the tooth centrally slightly concave. First and second upper molars (m$^{1-2}$) with hypocone markedly lower than the protocone, the hypoconal basin of m^1 more or less contiguous with the protoconal basin, the two basins in m^2 slightly more sharply demarcated from each other in teeth with little wear, the rear face of each tooth sharply concave in its central part, isolating the hypocone and metacone to some extent, and producing a wide space between the medio-posterior part of the tooth and the anterior face of the succeeding tooth. Third upper molar (m^3) reduced, the metastyle, metacone and hypocone lost, the mesostyle present but displaced internally, only the first ridge or paracrista and a reduced second ridge or post-paracrista remaining, the latter terminating at the mesostyle which lies posteriorly in the centre of the rear margin of the tooth, the pre-metacrista and metacrista lost. Lower incisors (i$_{1-2}$) about equal in size, tricuspid, the central cusp slightly the larger, the teeth long and narrow, lacking any low posterior supporting cusps, not imbricated, i$_2$ separated from the canine by a small diastema. Lower canine with moderately long, slender shaft, rising from a narrow cingulum, with no accessory cusps. First lower premolar (pm$_2$) large, longer than wide, a little longer but slightly narrower than the second lower premolar (pm$_4$), with narrow cingulum and large cusp,

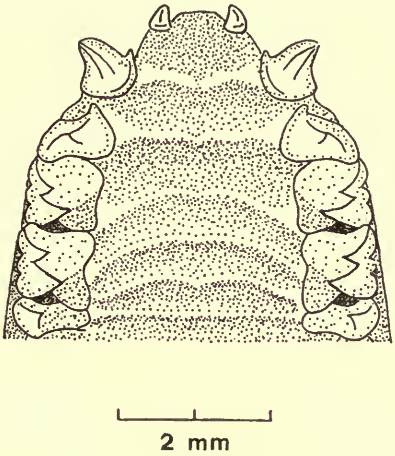

FIG. 6. *Craseonycteris thonglongyai.* ♂ TNRC 54-3872. Palate ridges.

triangular in lateral profile. Second lower premolar (pm_4) slightly compressed in toothrow, rather caniniform, its base about as long as wide, with narrow cingulum and tall, slender, rounded spike-like cusp, a little exceeding the height of pm_2 and equal in height to the first lower molar (m_1), the cusp hollowed posteriorly. Lower molars (m_{1-3}) with no especial peculiarities, m_3 a little reduced, its posterior triangle slightly smaller than the anterior triangle, the hypoconid and entoconid reduced.

Humerus (Fig. 7) with trochiter or greater tuberosity about as large as trochin or lesser tuberosity, extending proximally beyond the head of the humerus, trochiter with small articular surface on its posterior face, separated from head of humerus by a distinct groove, the articular surface of head extending across the groove to the ventral face of the trochiter ; trochin well developed but not reaching proximally to head of humerus which is rounded, not compressed laterally. Proximal face of humerus lacking distinct ridges, groove between trochiter and head of humerus deepened at its anterior end to form a shallow supraglenoid fossa. Anterior face of shaft of humerus flattened medianly in its proximal part, lacking any median deltoid ridge, instead a low but distinct elevation extending dorsad from the base of the trochiter to edge of flattened proximal part of shaft to form a short, narrow dorsal flange beneath the trochiter ; trochin similarly supported by a thin ventral flange extending along a short part of the opposite side of the shaft, which itself is slightly curved, the curve simple. Radial fossa indistinct ; capitellum slightly displaced

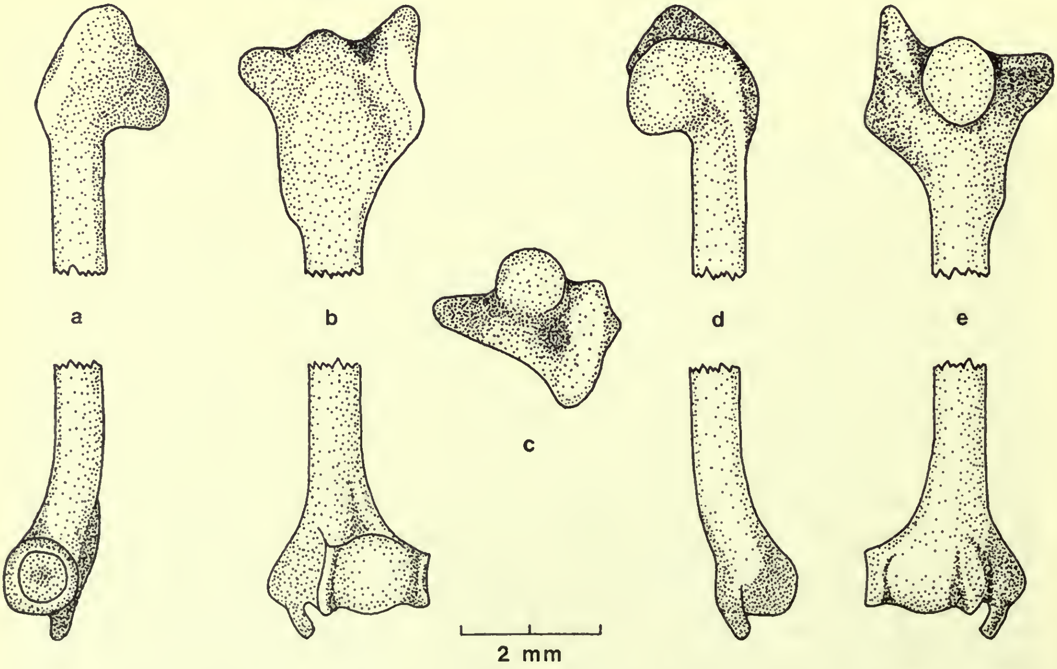

FIG. 7. *Craseonycteris thonglongyai.* ♂ TNRC 54-3865. Left humerus. a. Dorsal aspect. b. Anterior aspect. c. Proximal aspect. d. Ventral aspect. e. Posterior aspect.

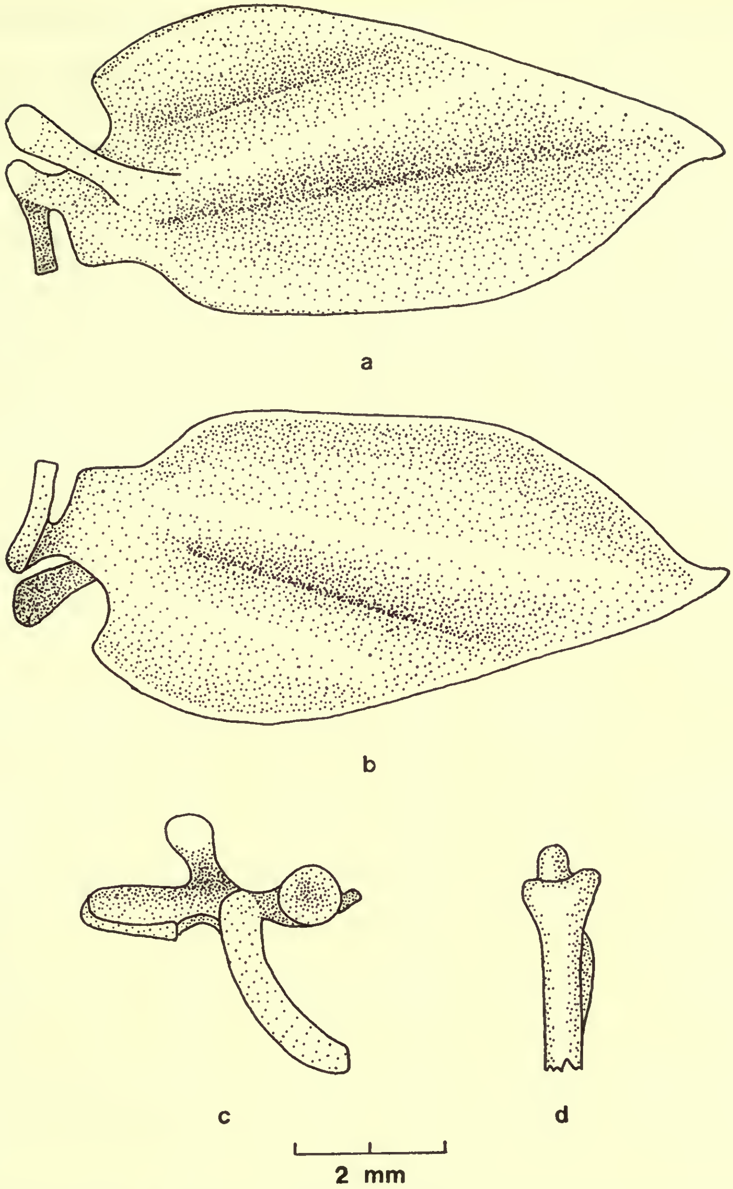

Fig. 8. *Craseonycteris thonglongyai.* ♂ TNRC 54-3865. a. Dorsal aspect of left scapula. b. Ventral aspect of left scapula. c. Anterior aspect of left scapula. d. Medial aspect of proximal end of left femur.

from line of shaft, its principal articular surface spherical, not compressed or oblique ; lateral surface narrow, not extending distally as far as the principal part of the capitellum ; trochlea similarly narrow, extending distally about as far as the principal articular surface ; epitrochlea or medial process about half as wide as distal articular surface, with small epitrochlear or distal spinous process, extending distally beyond the articular surface.

Sternum not especially modified; presternum or manubrium T-shaped, with broad, dorso-ventrally flattened lateral extensions or processes; anterior part of presternum with moderately developed keel, posterior extension broad, flattened dorso-ventrally, with low keel; mesosternum with longitudinal median ventral ridge; xiphisternum short, parallel-sided, with rounded tip, surrounded by cartilage. Clavicle slender; scapula (Fig. 8, a–c) large, elongate; supraglenoid tuberosity relatively well developed, with small articular face; coracoid border deeply notched, with narrow, ventrally directed flange; axillary border slightly notched behind glenoid fossa with a shallow postglenoid depression; acromion process slender, recurved antero-ventrally; coracoid process well developed, directed laterad, parallel-sided, its tip simple. Supraspinous fossa about one third the area of the infraspinous fossa, with no especial features; infraspinous fossa strongly faceted, the antero-medial facet wide, set at a sharp angle to the intermediate facet which is wide distally, the fossa divided more or less medianly by a deep, angular groove;

TABLE 1

External measurements (in mm) of *Craseonycteris thonglongyai*

		♂♂			♀♀		
	Holotype ♂ TNRC 54-3871	No. of specimens	Range	Mean	No. of specimens	Range	Mean
Width of narial pad	3·9	17	3·8–4·3	4·1	8	3·8–4·4	4·0
Width of narial ridge	2·2	17	1·9–2·4	2·2	9	2·0–2·5	2·2
Length of ear	9·6	17	9·0–10·0	9·5	9	9·0–10·2	9·8
Width of ear	7·9	17	7·3–8·5	7·9	9	7·3–8·3	7·9
Length of tragus	4·0	17	3·8–4·2	4·0	9	3·8–4·1	4·0
Length of tibia	12·3	16	11·9–12·9	12·3	9	11·7–12·8	12·3
Length of foot (with claw)	6·0	17	5·9–6·8	6·3	9	5·8–6·6	6·2
Length of forearm	24·4	16	24·1–25·2	24·6	9	22·5–25·8	24·9
Length of thumb	4·9	17	4·6–5·3	5·0	9	4·6–5·3	4·9
Length of II^m	25·0	17	24·1–25·6	24·7	9	23·9–26·5	25·6
Length of II^1	0·52	17	0·40–0·55	0·50	9	0·45–0·54	0·51
Length of II^d cartilage	0·63	17	0·40–0·63	0·52	9	0·42–0·60	0·51
Length of III^m	20·6	16	19·8–21·6	20·7	9	19·7–21·7	21·1
Length of III^1	6·9	17	6·4–7·0	6·7	9	6·5–7·1	6·8
Length of III^2	20·1	16	18·7–21·5	20·3	9	19·4–21·2	20·1
Length of IV^m	22·7	17	21·7–23·2	22·4	9	21·7–23·8	23·1
Length of IV^1	3·9	17	3·5–4·2	3·9	9	3·6–4·3	3·9
Length of IV^2	10·3	17	9·7–10·7	10·2	9	9·7–10·8	10·3
Length of V^m	22·7	17	21·7–23·0	22·4	9	21·8–23·7	23·2
Length of V^1	5·7	17	5·2–5·7	5·4	9	5·2–5·9	5·6
Length of V^2	6·0	16	6·1–7·0	6·3	9	5·9–6·6	6·2

The nomenclature used for the digits in this Table, in Table 3 and in Table 4 is an extension of Andersen (1905: 246, footnote), i.e. III^d is the third digit, III^m its metacarpal, and III^1 and III^2 its first and second phalanges.

TABLE 2

Cranial measurements (in mm) of *Craseonycteris thonglongyai*

	Holotype ♂ TNRC 54-3871	♂♂			♀♀		
		No. of specimens	Range	Mean	No. of specimens	Range	Mean
Greatest length of skull	11·1	11	10·6–11·5	11·2	5	10·3–11·1	10·9
Condylocanine length	9·9	12	9·9–10·1	10·0	5	9·6–10·0	9·9
Condylobasal length	10·0	11	10·0–10·3	10·1	5	9·5–10·1	9·8
Palatal length	4·0	11	3·9–4·2	4·1	5	3·8–4·1	3·9
Palatilar length	3·8	11	3·7–3·9	3·8	5	3·6–3·9	3·7
Width across ante-orbital foramina	3·8	12	3·7–4·0	3·9	5	3·7–3·9	3·8
Width across lacrimals	4·4	12	4·3–4·6	4·4	5	4·2–4·5	4·4
Width across rostral swellings	4·1	12	4·0–4·4	4·1	5	3·9–4·3	4·1
Zygomatic width	5·8	12	5·5–6·0	5·8	5	5·5–5·7	5·6
Postorbital width	2·2	12	2·1–2·3	2·2	5	2·1–2·2	2·1
Width of braincase	5·6	12	5·3–5·7	5·5	4	5·4–5·5	5·5
Height of braincase	4·1	12	4·0–4·3	4·1	4	3·9–4·0	4·0
Mastoid width	5·8	12	5·7–6·0	5·8	4	5·7–5·9	5·8
c^1–c^1	3·0	12	2·9–3·2	3·0	5	2·8–2·9	2·8
m^3–m^3	4·6	12	4·6–4·9	4·7	5	4·5–4·6	4·6
Post-palatal width	1·5	12	1·4–1·5	1·5	5	1·4–1·5	1·4
Width across pterygoid wings	1·8	7	1·8–2·0	1·9	5	1·7–2·0	1·8
Length of tympanic bulla	2·6	12	2·4–2·7	2·6	5	2·3–2·6	2·6
Width of tympanic bulla	1·8	11	1·5–1·9	1·7	5	1·6–1·8	1·7
Length of cochlea	2·1	12	1·8–2·2	2·0	5	1·8–2·2	2·0
Width of cochlea	2·2	12	2·0–2·3	2·2	5	2·0–2·1	2·1
Width of basioccipital	0·6	12	0·5–0·7	0·6	5	0·5–0·6	0·6
c–m^3	3·8	12	3·7–3·9	3·8	5	3·6–3·8	3·7
Length of complete mandible	6·9	12	6·9–7·1	7·0	4	6·7–6·9	6·8
Length of right ramus	7·0	12	7·0–7·3	7·1	4	6·9–7·1	7·0
c–m_3	4·0	12	4·0–4·2	4·1	5	3·9–4·0	4·0

postero-lateral facet about as wide as intermediate facet, with proximally a low ridge extending from the base of the glenoid fossa along but just within the axillary border and distally along the further two thirds of the axillary margin ; ventral surface of scapula with four facets, underside of postero-lateral facet rather narrow.

Last cervical vertebra not fused to first thoracic ; lower three thoracic vertebrae fused, their boundaries faintly visible ; lumbar vertebrae except last two solidly ankylosed, the last two free ; sacral vertebrae fused, their boundaries obliterated or nearly so ; two small caudal vertebrae. Pelvis small, weak, the ilia long and very slender ; ascending ramus of pubis short, the depth of the pelvis less than one half of its total length ; no definite acicular or pubic spine ; ventral ramus of pubis thin and delicate ; ischium with similarly thin, delicate ascending ramus, these structures easily lost. Femur (Fig. 8, d) slender, delicate, its proximal part not markedly deflected, with strong flange on its anterior face ; trochanters small but evident, the lesser trochanter slightly the larger and extending proximally a little further than the greater trochanter. Fibula thread-like, tapered, extending about halfway along the tibia.

Measurements of *Craseonycteris thonglongyai* appear in Tables 1 and 2.

REMARKS. The species is named to commemorate the late Kitti Thonglongya, formerly Curator of Terrestrial Vertebrates at the Centre for Thai National Reference Collections, whose last discovery it was. His untimely death was a sad loss to his many friends and to mammalogy in southeastern Asia, especially in Thailand where his enthusiasm and energy will be greatly missed.

The suiform muzzle of *Craseonycteris thonglongyai* has suggested (H. Elliott McClure, in litt.) the vernacular name 'Hog-nosed bat' for this species : it has also been described (J. T. Marshall, in litt.) as the 'Bumble-bee bat'.

REVIEW OF DIAGNOSTIC FEATURES

The current taxonomic arrangement of the Chiroptera derives largely from the work of Miller (1907) who based the higher categories largely on the structure of the shoulder girdle, the humerus, sternum, spine and pelvis, and of the skull and teeth, remarking (p. 45) that 'in a group of characteristically volant animals the chief taxonomic importance must be assigned to the development of the wings'. More recently, Walton & Walton (1970) and Vaughan (1970a) have reviewed the structure of the skeleton among the families of bats and Slaughter (1970) has examined their dentition. Smith (1972) has reviewed a number of characters valuable in the classification of bats at the familial level and in examining the New World families relied greatly upon a more detailed examination of the humerus, the femur and tragus than did Miller, together with a lesser emphasis upon such features as acoustic emissions, hair structure, karyotypes, the histology of facial glands, ectoparasites, brain size and immunology, not always readily available to the systematist. The nature of the available material of *Craseonycteris* at present limits any study of the genus from the familial standpoint chiefly to the traditional characters employed by Miller, and to these have been added a number of features that seem relevant when considering the familial position of this unusual bat. A synopsis of the diagnostic features in the families of bats, with much other information, is given by Koopman & Cockrum (1967).

Muzzle

The muzzle of *Craseonycteris* resembles that of the Rhinopomatidae (which includes but one genus, *Rhinopoma*) in several respects. As in that family the muzzle is laterally swollen and the nostrils open directly anteriorly in a thickened narial pad, which is surmounted by a low dermal ridge. The nostrils, however, differ sharply : in the Rhinopomatidae they are slit-like and valvular (usually closed in preserved specimens) and situated quite closely to the upper margin of the narial pad, inclined at about 30 degrees to the horizontal. In *Craseonycteris* the nostrils are wide, the inner margin straight, the outer margin sharply curved and they lie nearer to the upper lip, set more sharply to the horizontal at an angle of about 60 degrees. There is no definite internarial septum in the Rhinopomatidae, and the superior dermal ridge is basically an extension of the narial pad ; in *Craseonycteris* the nostrils are separated by a clearly defined internarial septum which broadens in its upper part to form the base of a narrow superior dermal ridge extending over the central part of the narial pad, above the nostrils, and not completely across the pad as in the Rhinopomatidae. Among the Emballonuridae the nearest approach to *Craseonycteris* in the structure of the anterior muzzle is found in *Balantiopteryx* in which the nostrils are of similar shape and open anteriorly in the face of an anteriorly directed, nearly vertical pad and are separated by a wide septum, but there is no superior dermal ridge.

It may be conjectured that the low superior dermal ridge in *Craseonycteris* and perhaps in the Rhinopomatidae represents a rudimentary form of nose-leaf. A broadly similar but more developed structure occurs in the Vespertilionidae (in the subfamily Nyctophilinae), while in the Hipposideridae the broadened upper part of the internarial septum forms the base of the central part of a sometimes complex nasal foliation. Furthermore, among the Phyllostomatidae the spear-like nose-leaf is a direct extension of the anterior muzzle.

Tragus

The tragus of *Craseonycteris* is well developed as it is in the Rhinopomatidae, but tapered distally and not truncate as in that family. Among the Emballonuridae the tragus is spatulate or pyriform. In *Craseonycteris* the tragus is remarkable for the curious oblate swelling at the mid-point of its anterior part, common to both male and female specimens. A slight swelling of the anterior part of the tragus is sometimes to be found in the Rhinopomatidae.

Wing structure

This in *Craseonycteris* provides a number of interesting features deserving further comment. The propatagium is broad and unusually large, a feature associated by Vaughan (1970b : 210) with hovering flight, in allusion to the glossophagine bats. In this respect *Craseonycteris* differs sharply either from the Rhinopomatidae or from the Emballonuridae, in which the propatagium is narrow. The relation of the second and third metacarpals and their associated phalanges to the intervening wing membrane that they support follows a similar pattern in *Craseonycteris* and in the Rhinopomatidae, although the method of support differs. In *Craseonycteris* and in the Rhinopomatidae that part of the wing membrane lying between the second and third digits tapers from the end of the second digit to terminate distally about one quarter or a little more of the distance along the second phalange of the third digit from its junction with the first phalange. In the Rhinopomatidae this part of the membrane is supported anteriorly by a second digit with a metacarpal similar in length to the third metacarpal, together with two relatively long phalanges : the total length of the digit is equal almost to the combined lengths of the third metacarpal and its first phalange. A similar arrangement prevails in *Craseonycteris* although achieved in a different fashion: the second metacarpal is much longer than the third metacarpal, the very short phalange and its cartilaginous appendage contributing little to the total length of the second digit, which equals or slightly exceeds the combined lengths of the third metacarpal and its first phalange. In the Emballonuridae this part of the leading edge of the wing is relatively shorter, the membrane between the second and third digits terminating distally on the third digit at or about the junction of its first and second phalanges and supported solely by the second metacarpal which is shorter than the third metacarpal, although only slightly so.

The second digit in the Rhinopomatidae has two well-developed bony phalanges: this digit in the Emballonuridae, Nycteridae, Rhinolophidae, Hipposideridae, Natalidae, Furipteridae and Thyropteridae lacks phalanges while the Myzopodidae have a cartilaginous rod. The second digit in the remaining extant families of the Microchiroptera has one bony phalange but it is minute in the Mystacinidae and rudimentary in the Noctilionidae and Molossidae. In *Craseonycteris* the second digit has one very short, insignificant bony phalange, usually integrated with the metacarpal, tipped with a short cartilaginous appendage. As in *Craseonycteris*, there is no distinct third phalange on the third digit in the Rhinopomatidae, Emballonuridae, Nycteridae, Megadermatidae, Rhinolophidae, Hipposideridae and Noctilionidae. The third phalange is cartilaginous, but ossified at its extreme base, in the Natalidae, Furipteridae, Vespertilionidae and Molossidae: in the remaining extant Microchiropteran families the third digit has three bony phalanges.

In the graduation of the metacarpals, *Craseonycteris* differs quite markedly either from the Rhinopomatidae or from the Emballonuridae. In *Craseonycteris* the second metacarpal is the longest, the third the shortest, the fourth a little longer than the third and the fifth about as long as the fourth. In the Rhinopomatidae the second and third metacarpals are similar in length, the fourth considerably shorter, with the fifth longer and similar in length to the second and third. Among the Emballonuridae, the second is shorter than the third, the fourth yet shorter and the fifth the shortest: the tendency to shorten the fifth metacarpal in relation to the third and fourth is more pronounced among the larger genera. The relative wing proportions of many of the families of living Microchiroptera were studied by Revilliod (1916, tabs. 1–5) who for numerous species expressed the lengths of the individual components of digits three to five as a percentage of the length of the forearm: the relative wing proportions for *Craseonycteris* are given in Table 3. The pattern of third metacarpal the shortest of metacarpals three to five, followed in length by the fourth metacarpal and with the fifth subequal to or longer than the fourth occurs most frequently in the Megadermatidae, the Rhinolophidae, infrequently in the Hipposideridae and in some Phyllostomatidae.

The length of the first phalange of the third digit in *Craseonycteris* is a little more than one quarter of the forearm length. In this respect *Craseonycteris* differs sharply from the Rhinopomatidae in which the length of the phalange is one sixth or less of the length of the forearm. The Furipteridae (not studied by Revilliod) also have a very short phalange, similar in relative length to that of the Rhinopomatidae. Among the Emballonuridae the length of the phalange varies from about one quarter to two fifths of the forearm length: in the Diclidurinae (not studied by Revilliod), however, the phalange is very short, like that of the Rhinopomatidae. In the Rhinolophidae, Hipposideridae, Noctilionidae, Mormoopidae, Desmodontidae and Mystacinidae the relative length of the phalange varies from a little less than one fifth to one third or slightly more of the length of the forearm: in the remaining Microchiropteran families the phalange is usually relatively rather longer although in some Phyllostomatidae its length may barely exceed one quarter of the forearm length. The second phalange of the third digit in *Craseonycteris* is exceptionally long, more than three quarters the length of the forearm and similar in length to the third metacarpal. In the length of this phalange *Craseonycteris* differs widely from the Rhinopomatidae, in which the phalange is about one third of the forearm length, or from the Emballonuridae, in which the phalange, although relatively longer in some species, only rarely equals one half of the forearm length. The relative length of the second phalange of the third digit in *Craseonycteris* is equalled only by the Noctilionidae, and, in the Vespertilionidae, by the Miniopterinae, although it is equalled or exceeded by the combined lengths of phalanges two and three in some Mormoopidae, by some species of Phyllostomatidae, notably in the Carolliinae and Stenoderminae, and by one of the genera of Desmodontidae. The Megadermatidae, some Kerivoulinae among the Vespertilionidae and some Molossidae approach *Craseonycteris* in the relative length of the second phalange of the third digit. Furthermore, in *Craseonycteris* this unusually long phalange is reflexed beneath the wing in specimens preserved in alcohol: reflexion of the proximal phalange of the third digit above the wing occurs in the Emballonuridae, Mystacinidae and Molossidae, and of the terminal phalange below the wing in the Noctilionidae and, among the Vespertilionidae, in the Miniopterinae.

The extreme shortness of the first phalange of the fourth digit in *Craseonycteris*, where it is about one sixth of the length of the forearm, is also an unusual feature. In the Rhinopomatidae the phalange is one fifth or more of the forearm length, and as a rule similarly so in the Emballonuridae, although exceptionally in this family the phalange may be a little less than one fifth of the length of the forearm. Among the remaining Microchiropteran families the Noctilionidae and rarely some Rhinolophidae resemble *Craseonycteris* in this respect. The first phalange of the fourth digit is relatively only a little longer in some others of the Rhinolophidae, in some species of the Mormoopidae and Desmodontidae, and in the Furipteridae. The second phalange of the fourth digit is shorter than the first phalange in the Rhinopomatidae, the Emballonuridae, Nycteridae, Thyropteridae (not studied by Revilliod) and Molossidae: in the Hipposideridae it is generally shorter than the first phalange, as it is with some exceptions, notably the Miniopterinae, in the Vespertilionidae. Otherwise, the second phalange of the fourth digit is longer than the first phalange: in *Craseonycteris* it is very long, its length exceeding two fifths of the length of the forearm and equalled in this respect only by the Noctilionidae and Miniopterinae. As in these, the terminal phalange is reflexed beneath the wing in specimens preserved in alcohol.

The first phalange of the fifth digit in *Craseonycteris* is about one quarter the length of the forearm : in the Rhinopomatidae this phalange is very short, about one sixth of the forearm length and in the Emballonuridae rather longer, generally a little less than one quarter of the length of the forearm but on occasion as long as nearly one third of the forearm length. In the remaining extant Microchiropteran families the length of the phalange is generally between one fifth and one third or a little more of the length of the forearm but in certain of the Noctilionidae, some Mormoopidae and Desmodontidae and in some Vespertilionidae the relative length of the phalange is less than one fifth of the forearm length and the Mystacinidae in particular have a very short phalange, like the Rhinopomatidae. The second phalange of the fifth digit is longer than the first phalange, as in *Craseonycteris*, in the Megadermatidae, Rhinolophidae, some Hipposideridae, some Mormoopidae and Phyllostomatidae, the Desmodontidae, some Natalidae, the Mystacinidae and rarely in the Vespertilionidae. Otherwise it is equal to or shorter than the first phalange.

Revilliod (1916) summed the relative lengths of each digital component to provide a relative indication of the total length of each digit. This technique shows *Craseonycteris* (Table 3) to have a wing with broadly the same proportions as the wing of the Nycteridae. The Rhinopomatidae, Emballonuridae, Mormoopidae and Mystacinidae have digital proportions falling short of those for *Craseonycteris* : the proportions for digits three and four in *Craseonycteris* agree closely with the Noctilionidae but this family has a shorter fifth digit. The Rhinolophidae, Hipposideridae (except for digit five in *Coelops*) and Furipteridae also have relatively shorter digits. The digital proportions in the Megadermatidae, the Myzopodidae and the Thyropteridae approach those of *Craseonycteris*, as do some Phyllostomatidae and certain of the Desmodontidae and Natalidae : others of the same families exceed them. For the most part the proportions for digits three and four in *Craseonycteris* are exceeded by the Vespertilionidae but for digit five only by the Murininae and Kerivoulinae. Similarly, in the Molossidae the relative proportions for digits three and four exceed those of *Craseonycteris*, but digit five in the Molossidae is much shorter. In general terms, the wing of *Craseonycteris* is relatively wide and long, with a long tip.

In the same paper, Revilliod attempted to demonstrate the degree of adaptation to flight in the families that he examined by means of an index obtained by subtracting the length of digit five as a total percentage of the forearm length from the total percentage length of digit three. This technique emphasizes the position of species with long narrow wings in relation to those with short, broad wings : as might be expected, the Molossidae, some Vespertilionidae and some Phyllostomatidae occupy the highest positions with the greatest values of the index, but the results obtained display wide variation with some Vespertilionidae and some Phyllostomatidae in relatively low positions. This is perhaps inevitable when one aspect only of the chiropteran wing is examined. The figure obtained for *Craseonycteris* (Table 3) is low, its wing, although long, being comparatively wide, a combination obscured in the index employed by Revilliod.

More recently, the morphological properties of the chiropteran wing have been examined in some detail by Findley, Studier & Wilson (1972). These authors have studied the relation between certain properties of the bat wing to the mode of flight.

In particular, the aspect ratio (length from wrist to tip of third digit plus length of forearm, divided by width at fifth digit) and the tip index (length from wrist to tip of third digit, divided by the length of the forearm) seem especially relevant when considering *Craseonycteris*. In this genus (Table 3) the aspect ratio proves to be somewhat below the average demonstrated by Findley, Studier & Wilson (1972 : 430, tab. 1, 434, fig. 1) for all bats. However, the tip index is very high, placing *Craseonycteris* among those bats (glossophagines, murinines, kerivoulines) which hover or are thought to do so, or are migrants or high speed foragers (miniopterines, lasiurines, molossids) (loc. cit. p. 430, tab. 1, 436, fig. 2, 437). Furthermore, Findley, Studier & Wilson suggest (p. 437) that the combination of a below average aspect ratio with a high tip index is especially suited for hovering flight, as might be the elongate wing tip. In the Rhinopomatidae there is a complete contrast : according to Findley, Studier & Wilson (p. 430, tab. 1, 434, fig. 1) *Rhinopoma* has a below average aspect ratio, combined with the lowest tip index of any bat studied (p. 430, tab. 1, 436, fig. 2) and, according to Harrison (1964 : 62) has an unusual, fluttering, undulating flight. Little is known of the mode of flight of the Emballonuridae, but in this family the aspect ratio was found by Findley, Studier & Wilson (p. 430, tab. 1, 434, fig. 1) to be considerably above the average for all bats, and the tip index (p. 430, tab. 1, 436, fig. 2) well below.

While variation in the proportions of the wing in the various Microchiropteran families is such that these features evidently cannot be used as a ready and reliable

TABLE 3

Wing proportions (forearm = 100) and wing characteristics for *Craseonycteris thonglongyai*

		♂♂			♀♀		
	Holotype ♂ TNRC 54-3871	No. of specimens	Range	Mean	No. of specimens	Range	Mean
II^{m}	102·5	16	97·2–102·8	100·1	9	100·0–106·2	102·5
III^{m}	84·4	16	81·9–86·7	84·3	9	82·5–87·5	84·2
III^{1}	28·3	16	26·1–28·5	27·3	9	26·1–29·3	27·2
III^{2}	82·4	15	74·5–88·0	82·4	9	76·2–86·7	80·7
III^{d} total	195·1	14	183·9–201·4	193·4	9	185·8–203·5	192·6
IV^{m}	93·0	16	88·6–93·2	90·8	9	90·3–96·4	92·8
IV^{1}	16·0	16	14·7–16·9	15·7	9	14·5–16·9	15·5
IV^{2}	42·2	16	39·0–44·2	41·5	9	39·9–43·4	41·4
IV^{d} total	151·2	15	144·5–152·5	148·4	9	145·8–156·4	149·7
V^{m}	93·0	16	88·6–93·0	90·9	9	91·0–96·9	92·9
V^{1}	23·4	16	20·8–23·4	22·0	9	20·3–23·2	22·4
V^{2}	25·0	15	24·5–28·5	25·7	9	23·0–28·0	24·8
V^{d} total	141·4	14	136·1–143·0	138·6	9	137·1–148·0	140·0
III^{d} total–V^{d} total	53·7	14	47·2–61·5	54·8	9	46·5–58·1	52·6
Aspect ratio	2·09	14	2·06–2·17	2·11	9	2·05–2·15	2·09
Tip index	1·95	15	1·84–2·01	1·95	9	1·85–2·03	1·92

Aspect ratio= III^{d} from wrist to tip + forearm/width at V^{d}.
Tip index= III^{d} from wrist to tip/forearm.
(III^{d} from wrist to tip= III^{m} + III^{1} + III^{2}; width at V^{d}= V^{m} + V^{1} + V^{2}.)

guide to classification at the familial level, it is clear that *Craseonycteris* cannot be allied closely either to the Rhinopomatidae or to the Emballonuridae from the structure of its wing, and that it is adapted for a quite different mode of flight from either of these. The relative proportions of digits three to five in *Craseonycteris* correspond reasonably closely to those of the Nycteridae (Revilliod, 1916 : 164, tab. 1) or with certain of the Phyllostomatidae (loc. cit. p. 170, tab. 3). The broad wing of *Craseonycteris* does not imply a bat adapted for fast or sustained flight, and, indeed, the structure of the wing suggests a hovering or at least a partially hovering species.

Tail

The tail is variable in the Microchiroptera. It may be present or absent (even within the family) ; its length may exceed the length of the uropatagium, or it may be subequal to this membrane in length or sometimes shorter, enclosed or partially enclosed within it, on occasion projecting from the posterior margin of the uropatagium or emerging through its upper surface. The Rhinopomatidae are unique among the living families in the presence of a long, slender, mouse-like tail, emerging from the edge of a reduced uropatagium. In the Emballonuridae the tail is shorter than the uropatagium and its free tip emerges through the upper surface about halfway or a little less along the length of the membrane. There is no external tail in *Craseonycteris*, but the uropatagium is moderate and rather full, an unusual feature in a tail-less species : Vaughan (1970b : 214) remarked that a large uropatagium is found in some 'flycatcher' bats which forage near the ground or among vegetation, and which also have broad wings.

Calcar

As in the Rhinopomatidae, the uropatagium of *Craseonycteris* lacks calcarial support. Generally present in the Microchiroptera, the calcar is short or absent in some species of Phyllostomatidae, and rudimentary (on occasion not connected with the membrane) in the Desmodontidae, but in these the uropatagium is reduced : its absence in a species with a moderate membrane is unusual.

Throat glands and pubic nipples

Throat glands are found in the Emballonuridae, Phyllostomatidae, Vespertilionidae and the Molossidae, often associated with a pouch or sac (Quay, 1970 : 23) : pubic nipples have been reported from the Rhinopomatidae, Megadermatidae, Nycteridae, Rhinolophidae, Hipposideridae, from the Nyctophilinae among the Vespertilionidae and possibly the Phyllostomatidae (loc. cit. p. 27).

Lateral rostral swellings

The rostrum is variously swollen or inflated in a number of Microchiroptera. Lateral rostral swellings, however, are noticeably characteristic of the Rhinopomatidae and Emballonuridae. In the Rhinopomatidae the swellings extend anteriorly beyond the narial aperture : those of *Craseonycteris* more nearly resemble the lateral swellings of the Emballonuridae.

Premaxillae

The structure of the premaxillae in *Craseonycteris* is unique, although it has clearly an overall resemblance to the arrangement found in the Rhinopomatidae and Emballonuridae. In neither of these, however, do the premaxillae fuse anteriorly, although as in *Craseonycteris* they are free from the adjacent parts of the skull, with the palatal branch short or absent, nor do their well-developed narial branches ever reach dorsally to the apex of the narial aperture and fuse together. In some Emballonuridae the premaxillae may lie partially on the surface of the maxillae, especially in *Taphozous* in which there is a very distinct approach towards the condition found in *Craseonycteris*. In *Taphozous* the ascending part of the narial branch is greatly developed and widened in its upper part, extending dorsad almost to enclose the narial aperture, the two premaxillaries separated at the apex of the aperture by a distance of about one third of the total width of the aperture. Posteriorly, the upper part of each narial branch is deflected into a narrow plate or lamina which lies on the surface of the maxilla. The inner edge of the narial branch is thrust forward anteriorly to form a sub-tubular flange at the side of the narial aperture, extending upwards to the outer upper part of the opening and terminating at the central division between the two branches. The premaxillae, therefore, form a structure similar in many ways to that prevailing in *Craseonycteris*, that is, a more or less tubular anterior projection partially surrounding the narial aperture, rising from a basal plate which rests on the maxillae and nasals, except that in *Taphozous* the surrounding ring and plate is incomplete, the narial branches failing to meet and fuse at the apex of the narial opening. The structure is rather less developed in *Taphozous* (*Saccolaimus*) than in *T.* (*Taphozous*) or *T.* (*Liponycteris*). In some other genera of Emballonuridae, for example in *Coleura*, *Saccopteryx* or *Diclidurus*, the narial branch of each premaxilla is widened to lie on the maxilla. A further stage from *Taphozous* is found in the Noctilionidae where the premaxillae are fused anteriorly and to the maxillae : the narial branches are unusually long and well developed, forming the sides of strongly tubular nares, separated above by the nasals. A similar arrangement prevails among the Mormoopidae. It is perhaps permissible to speculate that the sub-tubular structure in *Craseonycteris* supports the narial pad to which it is firmly attached by tough tissue. The free premaxillae in the Rhinopomatidae, the Emballonuridae and in *Craseonycteris* may serve to increase the mobility of the upper lip and the anterior part of the mouth when seizing food. They may also fulfil a similar function in the Nycteridae, Rhinolophidae and Hipposideridae but in these the premaxillae are represented only by their palatal branches and are cartilaginous in the two latter families.

Dentition

The dentition of *Craseonycteris* is very similar to that of *Rhinopoma*, with only a few relatively minor differences. The most obvious of these are the relatively larger upper incisors, the presence of a small antero-internal canine cusp, and the slightly further reduced condition of the third upper molar. Slaughter (1970 : 66) stated that in the Rhinopomatidae (mis-headed Rhinolophidae) the third upper molar lacks the pre-metacrista and that the hypocones of the upper molars are completely separate from the protoconal basins. However, in the majority of specimens the third upper molar has, as Miller (1907 : 82) pointed out, a metacone, mesostyle and three commissures : the mesostyle is invariably displaced and the third commissure or pre-metacrista is very short, terminating in an ill-defined metacone. Wear rapidly erodes the third ridge and metacone. The hypoconal basin of the first upper molar is broadly contiguous with the protoconal basin and separated only by a low commissure soon eroded by wear : in the second upper molar the basins are more definitely separated particularly in teeth with little wear.

Humerus

Apart from the early study by Miller (1907), the humerus of bats is discussed in considerable detail by Walton & Walton (1970 : 105), Vaughan (1970a : 117 et seq.) and Smith (1972 : 16). According to Vaughan (1970a : 130) modifications of the humerus for improved wing control are proximally the enlargement of the trochiter, the development of a supraglenoid fossa and of a large medial or deltoid ridge and, distally, the development of an epitrochlear or distal spinous process. These features are considered in greater detail, but for New World families only, by Smith (1972 : 16 et seq.).

Proximal end of humerus

Among the Microchiroptera the Rhinopomatidae, Emballonuridae, Nycteridae and Noctilionidae are sometimes considered primitive in that the trochiter is not greatly developed and proximally does not extend significantly beyond the head of the humerus, and a supraglenoid pit is lacking in the proximal face of the humerus at the anterior edge of the head. To these, Vaughan (1970a : 131) adds that the medial ridge is weakly developed, but some of these have a prominent medial deltoid ridge. At the other extreme, the Vespertilionidae, Mystacinidae and Molossidae have a large trochiter which extends proximally well beyond the head, there is a deep supraglenoid fossa and the humerus has a substantial deltoid ridge. The remaining families form an intermediate group in which these characteristics are developed to varying degrees. The proximal extension of the trochiter apparently provides a locking mechanism which restricts the action of the humerus (Smith, 1972 : 28) rather than a 'secondary articulation' or 'double articulation' as Miller (1907) thought.

In *Craseonycteris* the trochiter is about as large as the trochin and extends proximally beyond the head of the humerus and a definite, deep supraglenoid fossa surrounded by the proximal part of a deltoid crest is lacking. Instead, the anterior part of the groove between the trochiter and the head of the humerus is deepened to provide a small fossa into which the supraglenoid tuberosity articulates. There is no deltoid ridge but the anterior face of the humerus is slightly elevated at the base of the trochiter, the elevation passing into a dorsal flange, and a similar ventral flange supports the trochin. The deltoid ridge is absent or very weak only in the Pteropodidae but in some Phyllostomatidae (*Micronycteris*, *Glossophaga*) and, among the Vespertilionidae in the Kerivoulinae, the deltoid crest is displaced dorsad, although only slightly so. The proximal end of the humerus in *Craseonycteris* thus differs sharply from those families considered primitive, and in the proximal extension of the trochiter approaches the Vespertilionidae. The lack of a definite deep supraglenoid fossa corresponds more closely to the allegedly primitive families, although the trochiter in *Craseonycteris* is separated from the head by a moderate groove with a shallow fossa, and the trochiter itself has small articular surfaces on its posterior face and on its ventral face opposite the humeral head. In *Craseonycteris* the head of the humerus is rounded, as in the Rhinopomatidae and in many of the other Microchiropteran families : it is elongate or oval in the Emballonuridae, Rhinolophidae, Hipposideridae and Noctilionidae, elliptical in the Megadermatidae and Mystacinidae and variable in the Phyllostomatidae.

Distal end of humerus

Certain features of the distal end of the humerus were employed by Miller (1907) in the familial classification of the Chiroptera. These included the size and position of the capitellum, the development of the lateral epicondyle or external condyle, of the trochlea or medial epicondyle and of the epitrochlea, sometimes called the internal condyle or medial process, and the presence or absence of an epitrochlear or distal spinous process. These structures are discussed in considerable detail by Smith (1972 : 16), in relation to the New World families, and by Felten, Helfricht & Storch (1973) to European species.

Capitellum, lateral epicondyle and trochlea

These articular surfaces may vary in shape, size and proportion, and also in their degree of displacement dorsally from the axis of the shaft of the humerus. Variations in shape, size and proportion seem to offer little of familial significance. As a rule the central part of the capitellum is spherical or slightly oblong and forms the greater part of the articular surface : the lateral epicondyle is narrow and the trochlea similarly undeveloped, each separated from the principal surface by shallow grooves. The trochlea may become widened as in *Diclidurus* of the Emballonuridae to equal in width the central part of the capitellum, or the central part of the capitellum may be narrowed as in *Mormoops* of the Mormoopidae. In distal extension the trochlea may equal the lateral epicondyle, extend beyond it or beyond either the lateral epicondyle or the principal surface of the capitellum. This type of articulation, with some slight modification, is found in the majority of the families of Microchiroptera, but not in the Vespertilionidae or Molossidae. In these the principal part of the capitellum is angular or narrowed, and is tilted diagonally, a condition faintly foreshadowed in the Rhinolophidae and Hipposideridae, in which the otherwise spherical principal surface tends to be narrowed distally, or in the Nycteridae, where it is slightly oblique. The articular surfaces in *Craseonycteris* correspond closely to the first of these patterns and indeed closely resemble the pattern found in the Rhinopomatidae, most Emballonuridae and the Phyllostomatidae.

The displacement of the articular surfaces also varies between families. The capitellum in the Rhinopomatidae is slightly but distinctly displaced from the line of the shaft : it is similarly or more dorsally displaced in the majority of Microchiropteran families excepting the Emballonuridae, the Vespertilionidae and the Molossidae, although in some, such as the Noctilionidae and the Mormoopidae, as in the Rhinopomatidae, the degree of displacement is slight. In the Rhinolophidae and to a lesser extent the Hipposideridae the capitellum is widely displaced dorsally. In *Craseonycteris* the articular surfaces are slightly removed from the line of the shaft as they are in the Rhinopomatidae.

Epitrochlea

The epitrochlea or medial process may display varying degrees of development and ventral extension. In the Rhinopomatidae and for the most part the Emballonuridae, the epitrochlea is short and broad, the ventral portion sometimes curled : a similar process occurs in the Rhinolophidae and Hipposideridae. In the Nycteridae, Megadermatidae and Noctilionidae the epitrochlea is more massive and projects rather further ventrally : the Mormoopidae have a moderately developed epitrochlea, while among the Phyllostomatidae the epitrochlea varies from a relatively poorly developed condition to one displaying a moderate degree of development and ventral extension. The small families Natalidae, Furipteridae, Thyropteridae and Myzopodidae have a broad but rather short epitrochlea. The Vespertilionidae and Molossidae present a sharp contrast in a small, undeveloped epitrochlea which projects ventrally only slightly beyond the lateral line of the shaft. The epitrochlea in *Craseonycteris* is similar to that of the Rhinopomatidae, most Emballonuridae, or to those of the less developed processes found among the Phyllostomatidae.

Epitrochlear process

This is the spinous process of Miller (1907) or the distal spinous process of Smith (1972 : 17) which this author defined as the process extending distally from the tip of the epitrochlea or medial process. A second type of process is encountered in some families, arising not definitely from the tip of the epitrochlea, but from its distal margin. A similar, less developed structure is found among certain Phyllostomatidae, notably in *Lonchorhina*. Smith (1972 : 21) advanced evidence to suggest that in this genus at least the structure is not homologous with the distal spinous process arising from the tip of the epitrochlea, but is a departure from the basically bilobed epitrochlea found in certain members of the family.

An epitrochlear process occurs in most of the Microchiropteran families, reaching an optimum in the Molossidae. It is absent from the Rhinopomatidae and absent or poorly developed in the majority of Emballonuridae although sometimes well developed as in *Taphozous* and *Diclidurus*. It occurs in the Rhinolophidae, Hipposideridae and Noctilionidae and is well developed in the Mormoopidae. The Phyllostomatidae have no epitrochlear process or at least only a weak development of it :

a broad, low process is found in the Natalidae, Furipteridae, Thyropteridae and Myzopodidae. In the Natalidae, Furipteridae and Myzopodidae the dorsal base of the process is closely adpressed against the rim of the trochlea. The process is low but strong, virtually forming a part of the rim of the trochlea, in the majority of the Vespertilionidae, but is particularly well developed in the Miniopterinae, to equal the condition found in the Molossidae, in which the process is long, projecting well beyond the articular surfaces, and closely adpressed to the trochlear rim: the Mystacinidae also have a well-developed process. In the Nycteridae and the Megadermatidae the process is of the second type described above: in these Miller (1907 : 100) described it as 'styloid' rather than spinous: a similar process is found in some Rhinolophidae. It is of some interest to remark that the process is widely removed from the trochlear edge in the Emballonuridae, Rhinolophidae, Hipposideridae, Nycteridae, Megadermatidae, Noctilionidae and Phyllostomatidae. A variety of positions to one in which the process is almost in contact with the rim is found in the Mormoopidae (Smith, 1972 : 19, fig. 4). In *Craseonycteris* the process originates from the tip of the epitrochlea rather than from its distal edge, and is removed from the trochlear rim. It is similar to the process found in the Rhinolophidae or Hipposideridae, or to the less advanced of the Mormoopidae.

Vaughan (1970a : 130) remarked that the epitrochlear spine is not evident in the Rhinopomatidae, Emballonuridae, Noctilionidae and Nycteridae and is only fully developed in the Vespertilionidae, Mystacinidae and Molossidae, with the other families occupying an intermediate position. He concluded (p. 131) that the primitive families lack the epitrochlear process while the advanced families possess it. However, the process is present in some of the allegedly primitive families, although in these it may take a rather different form from the process in those apparently more advanced. Vaughan (p. 132) further considered the development of the epitrochlear process a factor evolved in response to the need for lightening the distal parts of the wing so that the wings might be controlled more easily. A similar view is advanced by Smith (1972 : 23) who suggested that the process in the Mormoopidae and Molossidae forms part of an automatic flexing mechanism. It is perhaps not without significance that a well-developed process in one form or another occurs not infrequently in bats in which the third digit is elongated, even in families, for example, such as the Emballonuridae and Vespertilionidae in which the process either is not normally greatly developed or does not normally extend distally to any great extent.

Scapula

The modifications of the chiropteran scapula are briefly discussed by Walton & Walton (1970 : 100) and by Vaughan (1970a : 128). The scapula in *Craseonycteris* has a number of relatively unmodified features: it is rather narrow, the supraspinous fossa is relatively large and lies in the same plane as the post-spinous part of the blade, the anterior flange is weak and the coracoid process is directed laterad. The infraspinous fossa, however, is quite strongly faceted, so that while in most respects the scapula resembles that of the majority of Microchiropteran families, in this feature it tends towards those in which the scapula is more specialized, such as the Molossidae, or *Lasiurus* or *Miniopterus* of the Vespertilionidae. This feature occurs also in *Taphozous* of the Emballonuridae, and, in this genus, in addition, the area of the supraspinous fossa is reduced, with a strong anterior flange. There is also in *Craseonycteris* a degree of articulation with the trochiter.

Fusion of lumbar vertebrae

In this respect, *Craseonycteris* resembles the Natalidae or the Furipteridae, also small, delicately formed bats. However, vertebral fusion occurs in some genera of the Hipposideridae and also in *Kerivoula* of the Vespertilionidae. As Miller (1907 : 182) pointed out, the feature is of no value in determining familial position.

Proximal end of femur

The proximal end of the femur in *Craseonycteris* resembles the condition found in the Emballonuridae, with the lesser trochanter a little larger than the greater trochanter and extending a little further proximally. It differs from the Rhinopomatidae in which the lesser trochanter is similar in size to the greater trochanter but stands marginally a little lower. The head and neck of the shaft of the femur are not deflected from the line of the shaft as in the Rhinolophidae and Hipposideridae. There is considerable variability in the structure of the head of the femur among the Microchiropteran families (Smith, 1972 : 29, 30, fig. 8) but the femur has a more limited value in familial classification than has the humerus, although this author found the Mormoopidae to lack well-developed trochanters, in contrast to the other families that he had examined.

A summary of the more obvious characters discussed appears in Table 4.

SYSTEMATIC POSITION OF THE CRASEONYCTERIDAE

The new family Craseonycteridae resembles the Rhinopomatidae in some external features, some cranial characters and especially in the details of its dentition. In particular, the narial pad with rudimentary superior dermal ridge, the structure of the leading edge of the wing, the lack of calcarial support to the uropatagium, the swollen rostrum, the free premaxillae with prominent narial branch, the shape of the dental arcade and the architecture of the teeth themselves provide good characters in which it tends towards this monotypic family. At the same time, its unspecialized nostrils, large, independent ears, the tragus, the highly modified wing which contrasts sharply with the rather simple wing of the Rhinopomatidae, the lack of a tail and the features of the humerus, scapula and pelvis set it widely apart from the Rhinopomatidae. Although the new family has some features in common with the Emballonuridae, notably in the structure of the nostrils, the presence of rostral swellings and in the structure of the premaxillae which is clearly foreshadowed in some Emballonuridae, the Craseonycteridae differ widely from this family in many other features. Among these the tragus, the lack of a tail, the absence of postorbital processes and of basioccipital pits, the dentition and the organization of the shoulder joint seem particularly notable. Furthermore, the Craseonycteridae differ widely from the Emballonuridae in the overall structure and characteristics of the wing.

The Craseonycteridae differ so widely from the Nycteridae, Megadermatidae, Rhinolophidae and Hipposideridae that any close relation is most unlikely. There exist also wide differences from the Noctilionidae and Mormoopidae, especially in the form and structure of the rostrum, of the palate and teeth, and of the head of the humerus. As with all of these families, the premaxillae provide a major distinction between the Craseonycteridae and any of those remaining, although it also differs from these in numerous other features. However, in the structure of the humeral head the Craseonycteridae approach those families considered more advanced in this respect, beginning to some extent with the Phyllostomatidae and terminating with the Vespertilionidae, Mystacinidae and Molossidae, although the humerus in the Craseonycteridae is less modified in comparison with the last three of these. My conclusion is, therefore, that the Craseonycteridae must be classified with the Rhinopomatidae and Emballonuridae. The wing in the new family is clearly more modified than in either of these, perhaps for a mode of flight involving hovering, by the enormous extension of the third digit with the concomitant development of the humerus. For this reason the Craseonycteridae should follow the Rhinopomatidae and the Emballonuridae : few features of the new family suggest that it in any way intermediates between these two. It is more correct to say that it carries further features already apparent in one or other, or both, of these.

Current classification of the Chiroptera is usually based on Simpson (1945). This author assembled the families delineated by Miller (1907) into superfamilies. Smith (1972 : 39) remarked that these superfamilies were based on Winge's families as expressed in his work (1892) on the mammals of Lagoa Santa, Brasil, and that as a result the Noctilionidae were grouped with the Rhinopomatidae and Emballonuridae in the superfamily Emballonuroidea, while the mormoopids were carried as a subfamily of the Phyllostomatidae into the Phyllostomatoidea. However, Winge consistently (1892 : 24 ; 1923 : 235 ; 1942 : 271) placed *Noctilio* with the mormoopid genera in the Phyllostomatidae, although Simpson (1945 : 180) stated that his classification retains Miller's families but groups them into superfamilies which are those of Winge. Possibly in this instance in grouping the Noctilionidae with the Rhinopomatidae and Emballonuridae Simpson was influenced by the remarks of Miller (1907 : 97) where relationship between these families is suggested. The Craseonycteridae stand closer to the Rhinopomatidae and Emballonuridae than to either the Noctilionidae or Mormoopidae. For this reason the new family should be included with the rhinopomatids and emballonurids in any further grouping, preferably as a superfamily, the Emballonuroidea. Within this assemblage, the Craseonycteridae are the most advanced, especially in wing structure. Smith (1972 : 39 et seq.) advanced reasons for considering the Noctilionidae, Mormoopidae and Phyllostomatidae as three distinct families possibly forming another superfamily, the Phyllostomatoidea although he noted (p. 41) that this grouping seemed premature.

TABLE 4

Summary of major familial and other characters discussed in text

	Rhinopomatidae	Emballonuridae	Craseonycteridae	Nycteridae	Megadermatidae	Rhinolophidae	Hipposideridae	Noctilionidae	Mormoopidae	Phyllostomatidae	Desmondontidae	Natalidae	Furipteridae	Thyropteridae	Myzopodidae	Vespertilionidae	Mystacinidae	Molossidae
Nostrils slit-like, valvular	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
Narial pad with dermal ridge	+	−	+	−	−	−	−	−	−	−	−	−	−	−	−	±	−	−
Nasal foliations	−	−	−	+	+	+	+	−	−	+	+	−	−	−	−	±	−	−
Tragus	+	+	+	+	+	−	−	+	+	+	+	+	+	+	+	+	+	+
Number of bony phalanges in II^d	2	0	1	0	1	0	0	1	1	1	1	0	0	0	0	1	1	1
Number of bony phalanges in III^d	2	2	2	2	2	2	2	2	3	3	3	2	2	3	3	2	3	2
Reflexion of proximal phalange of III^d above wing	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	+
Reflexion of terminal phalange of III^d below wing	−	−	+	−	−	−	−	+	−	−	−	−	−	−	−	±	−	−
Reflexion of terminal phalange of IV^d below wing	−	−	+	−	−	−	−	+	−	−	−	−	−	−	−	±	−	−
External tail	+	+	−	+	±	+	+	+	+	±	−	+	+	+	+	+	+	+
Calcar	−	+	−	+	+	+	+	+	+	±	+	+	+	+	+	+	+	+
Two phalanges only in toes II–IV	−	−	−	−	−	−	+	−	−	−	−	−	−	+	+	−	−	−
Pubic nipples	+	−	+	+	+	+	+	−	−	−	−	−	−	−	−	±	−	−
Postorbital processes	−	+	−	+	±	−	−	−	−	−	−	−	−	−	−	−	−	−

Premaxillae	+	+	+	+	−	+	+	+	+	+	+	+	+	+	+	+	+	+
Premaxillae fused to adjoining parts	−	−	−	−	−	−	−	+	+	+	+	+	+	+	+	+	+	+
Premaxillae complete	−	−	−	−	−	−	−	−	+	+	+	+	−	+	+	−	+	±
Palatal branches of premaxillae short or absent	+	+	+	−	−	−	−	+	−	−	−	−	+	−	−	+	−	±
Narial branches of premaxillae short or absent	−	−	−	+	−	+	+	−	−	−	−	−	−	−	−	−	−	−
Palatal branches of premaxillae fused	−	−	+	−	−	−	−	+	+	+	+	+	−	+	+	−	+	±
Narial branches of premaxillae fused posteriorly, lying on maxillae and nasals	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
Trochiter extending distally beyond head of humerus	−	−	+	−	−	+	+	−	+	+	+	+	+	+	+	+	+	+
Supraglenoid fossa in proximal face of humerus	−	−	+	−	−	+	+	−	+	+	+	+	+	+	+	+	+	+
Head of humerus rounded	+	−	+	+	−	−	−	−	−	+	+	+	+	+	+	+	−	−
Head of humerus oval	−	+	−	−	−	+	+	+	+	−	−	−	−	−	−	−	−	+
Head of humerus elliptical	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	+	−
Evident deltoid ridge	+	+	−	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Distal articular surfaces of humerus displaced from line of shaft	+	−	+	+	+	+	+	+	±	+	+	+	+	+	+	−	−	−
Narrow epitrochlea	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	+	+
Epitrochlear process	−	±	+	+	+	+	+	+	+	±	+	+	+	+	+	+	+	+
Sternum and shoulder girdle specialized	−	−	−	+	+	+	+	−	−	−	−	+	−	+	−	±	−	+
Last cervical and first thoracic vertebrae fused	−	−	−	+	+	+	+	−	−	−	−	−	−	−	−	±	−	+
First and second thoracic vertebrae fused	−	−	−	−	−	−	+	−	−	−	−	−	−	+	−	−	−	−
Lumbar vertebrae fused	−	−	+	−	−	−	±	−	±	−	−	+	+	−	−	−	−	−
Fibula well developed	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	+	+
Fibula absent	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−

+, Present. −, Absent. ±, Variable.

All are clearly distinct from the Rhinolophoidea, including the Nycteridae, Megadermatidae, Rhinolophidae and the Hipposideridae: the members of this superfamily have diverged considerably in different ways.

Smith (1972 : 40, 41) reviewed the possible phylogeny and evolution of the New World families Noctilionidae, Mormoopidae and Phyllostomatidae, and concluded that for various reasons the commonly accepted view that the Microchiropteran bats evolved from an emballonuroid-like ancestor might be challenged. The further corollary to this hypothesis is that the New World noctilionids, mormoopids and phyllostomatids derive from an Old World emballonuroid migrant or migrants. Instead, Smith postulated a 'palaeochiropteran' ancestor in both the Old and New Worlds, thus providing a base for an autochthonous lineage for the New World bat families with which he was concerned. The family Craseonycteridae presents little that can be described as truly intermediate between the Rhinopomatidae and Emballonuridae on the one hand and on the other hand the Noctilionidae, Mormoopidae and Phyllostomatidae. However, some features might be considered in this way: the low dermal narial ridge, for example, might be construed as an incipient nose leaf, or the sub-tubular premaxillae, which are foreshadowed in the Emballonuridae and reach a further stage in the Noctilionidae and Mormoopidae, might be thought to display an intermediate condition.

Slaughter (1970 : 66) discussed the origins of the rhinopomatid dentition and pointed out that it could conceivably have taken origin from within the Emballonuridae. However, the structure of the hypo-protoconal basins in the Rhinopomatidae indicated to this author that this dentition could derive directly from a superfamily prototype, or from incipient emballonurid stock, the latter seeming to him more probable. The conclusion that the dentition of the Rhinopomatidae derives at least from an ancestral prototype rather than from within the Emballonuridae is reinforced by the Craseonycteridae in which the rhinopomatid dentition appears, little changed, in a bat otherwise widely removed either from the Rhinopomatidae or from the Emballonuridae, and, indeed, much more widely removed from the Noctilionidae or Mormoopidae. The new family emphasizes the difficulties and dangers of inferring phylogeny from a variety of modern forms each of which exhibits a varying combination of different specializations and modifications in different degrees. All that can be said is that the Rhinopomatidae, Emballonuridae and Craseonycteridae had most probably a common ancestry.

Miller (1907 : 81) regarded the Rhinopomatidae as the most primitive of living microchiropteran families, largely on account of the presence of two phalanges in the second digit, the free premaxillae and the primitive shoulder joint. However, there is much to commend the views of Winge (1923 : 267 ; 1941 : 310) who considered *Rhinopoma*, the sole representative of the family, to be rather isolated among living bats. In many respects, he averred, it is highly specialized, as in its dentition, the form of the nasal cavity and the upper arm, while other features, such as the premaxillae and the presence of two phalanges in the second digit, indicated a primitive origin. Winge noted that Miller had stated that in *Rhinopoma* there is no 'secondary articulation' between trochiter and scapula but that in fact a narrow articulation is present. Indeed, the trochiter may on occasion very slightly exceed the head of the humerus. As Winge pointed out, Miller placed much emphasis on the features that he regarded as primitive. It has long been customary to associate the Rhinopomatidae with the Emballonuridae (Dobson, 1878 : 353 et seq. ; Winge, 1892 : 33 ; 1923 : 235 ; 1941 : 271 ; or Simpson, 1945 : 55) but there seems little in these features to suggest that the Rhinopomatidae are necessarily the more 'primitive'. The retention of two phalanges in the second digit of *Rhinopoma* may well be a corollary of the need to support a long leading edge of the wing, achieved in the Craseonycteridae by a relatively much longer metacarpal with insignificant phalangeal support : the simple shoulder joint with little modification of the proximal part of the humerus is perhaps a reflection of a correspondingly unspecialized wing. Furthermore, the valvular nostrils of *Rhinopoma* seem highly specialized : its long tail is an extreme of a variable chiropteran character and is possibly a 'primitive' feature although it may serve as a balancing organ in flight.

The Emballonuridae themselves are said by Miller (1907 : 84) to combine the greatest number of primitive characters with the least degree of specialization. Miller appears to have based this conclusion on the presence of postorbital processes, on the free premaxillae and the structure of the proximal part of the humerus. Yet the Emballonuridae display considerable modification of the premaxillae, varying from a comparatively simple condition in which the narial branches lie alongside the lateral margins of the narial aperture to the relatively advanced condition found in *Taphozous* in which a sub-tubular structure tending towards that found in the Craseonycteridae lies more or less on the surface of the maxillae. The deep basioccipital pits, sometimes divided by septa, seem also to be a specialized feature, and, as in the Rhinopomatidae, the number of teeth is reduced, although the process has not gone so far as in that family, only *Taphozous* among the Emballonuridae having lost one pair of lower incisors, while all emballonurids retain two upper premolars on each side. The wing in the Emballonuridae also presents some modification, with lengthening of the third digit in *Taphozous* and *Diclidurus*, and, throughout the family, with the flexing forward of its proximal phalange. The head of the humerus is slightly elongated and oblate in the Emballonuridae, rather than rounded, and slightly tilted, features possibly indicating a degree of specialization as Smith (1972 : 29) suggested for the Mormoopidae.

The Rhinopomatidae, with but a single genus, mostly inhabit arid or semi-desert regions in southern Asia and Africa : by contrast, the Emballonuridae are widely distributed in the tropical and sub-tropical parts of the Old and New Worlds, with numerous genera and species. The Craseonycteridae have a wing and shoulder structure very different from either of these families, showing evidence of modification for specialized flight, most probably of a hovering nature. Nevertheless, the family retains the rhinopomatid organization of the anterior edge of the wing, to a considerable extent the architecture of the rhinopomatid skull, and especially the rhinopomatid dentition, with the premaxillae modified in such a way as to represent the epitome of a tendency foreshadowed in the Emballonuridae. Free premaxillae are common to all three families and are found (as the palatal rather than the narial branches) also in the Nycteridae, Rhinolophidae and Hipposideridae. They may well provide a flexibility contributing to a feeding mechanism that requires considerable mobility of the upper lip and anterior mouth and are possibly of value to bats that glean insects. The enlarged trochiter of the Craseonycteridae suggests conventionally a relatively advanced bat, yet in the absence of an evident deltoid ridge or a definite deep supraglenoid pit it differs from the other families so considered, although in some of these the ridge may be displaced dorsad, and in some the supraglenoid pit is not exceptionally developed and is displaced dorsad to lie between the base of the humeral head and the trochiter, as in the Craseonycteridae. The development of an epitrochlear process seems a corollary of a need to operate and control a long wing with a long tip. My view is, therefore, that this new and striking family of bats represents a further branch of the Emballonuroidea, modified for a sophisticated style of flight, and thus combining some external, cranial and dental features similar to those of the Rhinopomatidae and Emballonuridae with some of the wing and skeletal features of those families considered conventionally more advanced. Such a combination is perhaps inevitable when the familial classification of the Order is based to some extent on modifications which improve the flying mechanism or adapt it to particular kinds of flight, reflecting Miller's dictum quoted above that in a group of characteristically volant animals the greatest taxonomic importance must be placed on the development of the wings.

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SUMMARY

A new family of bats, the Craseonycteridae, is proposed in the Microchiroptera for a new genus and species from Thailand, described as *Craseonycteris thonglongyai*. The new family is allied to the Rhinopomatidae and Emballonuridae and is placed in the Emballonuroidea. Its diagnostic features are reviewed in detail, with a discussion of its taxonomic position.

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